

STRUCTURE AND DISTRIBUTION OF DEMERSAL
FISH ASSEMBLAGES ON THE NORTHEAST
NEWFOUNDLAND AND LABRADOR SHELF

CENTRE FOR NEWFOUNDLAND STUDIES

**TOTAL OF 10 PAGES ONLY
MAY BE XEROXED**

(Without Author's Permission)

Ma GUADALUPE DEL MAR VILLAGARCÍA



STRUCTURE AND DISTRIBUTION OF DEMERSAL
FISH ASSEMBLAGES ON THE NORTHEAST
NEWFOUNDLAND AND LABRADOR SHELF

by

© M^a Guadalupe del Mar Villagarcía

A thesis submitted to the School of Graduate
Studies in partial fulfilment of the
requirements for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland
March 1995

St. John's

Newfoundland



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-612-13958-1

Canada

TABLE OF CONTENTS

ABSTRACT	iii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
CHAPTER 1. FISHERIES AND FISH ASSEMBLAGES	1
CHAPTER 2. MULTISPECIES DATA AND METHODS	6
2.1 Groundfish Data	6
2.2 Methods	11
CHAPTER 3. CHARACTERISATION OF THE FISH ASSEMBLAGES	16
3.1 Results of the Multispecies Analysis	16
3.1.1 Deep Assemblage	20
3.1.1.1 Description and Environmental conditions	20
3.1.1.2 Biomass and Species Composition	21
3.1.2 North Assemblage	23
3.1.2.1 Description and Environmental conditions	23
3.1.2.2 Biomass and Species Composition	25
3.1.3 Main Assemblage	27
3.1.3.1 Description and Environmental conditions	27
3.1.3.2 Biomass and Species Composition	29
3.1.4 Coastal Assemblage	32
3.1.4.1 Description and Environmental conditions	32
3.1.4.2 Biomass and Species Composition	33
3.2 Oceanography and Fish Assemblages	35
CHAPTER 4. TEMPORAL CHANGE OF FISH ASSEMBLAGES	38
4.1 Mean Situation	38
4.2 First Period: 1978-1986	38
4.3 Second Period: 1987-1991	44

CHAPTER 5. SPATIAL CHANGE OF FISH ASSEMBLAGES	49
5.1 Persistence and Fidelity	49
5.2 Possible Causes	51
5.3 Final Comments and Future Work	57
BIBLIOGRAPHY	59
APPENDIX 1.	List of total Autumn Species Biomass of each year over the study period
	67
APPENDIX 2.	Maps showing the distribution of bottom temperatures recorded each year in their geographical position
	91

ABSTRACT

Multivariate analysis of 14 years of scientific survey data has distinguished four groundfish assemblage areas on the Northeast Newfoundland and Labrador Shelf. The assemblages were characterized by an homogeneous faunal composition, and relative abundance and persistence over time. From 1978 to 1986, their spatial distribution was maintained within certain geographical boundaries which followed bottom topography and exhibit characteristic bottom temperature ranges. Starting in 1987 and coincident with a decline in the commercial fisheries, there was a shift of three of the assemblages towards the east. Further analysis revealed a decrease in biomass in all of the more abundant species as well as in some of the less abundant. Rare species were found to decrease earlier than dominant ones, perhaps acting as indicators of major changes taking place across the continental shelf. Increasing density of certain species near the shelf/slope break has produced groupings of fish offshore of the main banks which has made them more vulnerable to the fishery. Possible causes for this behaviour, e.g. varying bottom temperature and loss of stability in the main species, are investigated. Intense exploitation of groundfish is the most likely explanation for the decline of fish biomass on the Northeast Newfoundland and Labrador Shelf. Less abundant species distribution may also be affected by discard or as by-catch of the commercial species. The homogeneous fish assemblages found could be used as the basic units to manage the shelf in a smaller scale basis from a biological perspective and to define highly sensitive areas where fish tend to aggregate that might need to be protected.

ACKNOWLEDGEMENTS

I am indebted in every piece of my work to my supervisor, Dr. Richard Haedrich (Department of Biology, Memorial University), for patiently guiding me to build doubts and thoughts into this thesis. His perseverance and optimism have told me a lesson I will never forget.

I am also very grateful to Dr. Manuel Gomes (Faculty of Sciences, University of Lisbon, Portugal) for his guidance in the preliminary steps of my research and his long-distance presence to answer my numerous questions.

David Schneider (Ocean Sciences Centre, Memorial University) was always there to spare his time and mind-inspiring alternative points of view. Thank you!

I am very thankful to John Horne who helped my stay in Newfoundland from the beginning to the end providing every information and explanation needed.

Many thanks to all the "4 Clark Place" crowd that have helped me in many different ways. Especial thanks to Lynn Bussey and Jennifer Robinson for their help with handling the mountains of data.

Thank you Boyan for supporting me along my work.

Very special thanks to the staff of the Northwest Atlantic Fisheries Centre (Department of Fisheries & Oceans Canada) who compiled and made available the data I have used in this thesis.

My work in Canada since 1992 has been sponsored by a grant from "La Comunidad Canaria" and funding from the Ministerio de Educación y Ciencia (MEC), Madrid, Spain. Portions of this work were also supported by the DFO/NSERC Subvention Program, Ottawa, Canada.

I dedicate this work to my late brother Guillermo.

LIST OF TABLES

Table 1. List of species used in the analysis	9
Table 2. Number of years that each species appeared	10
Table 3. Biomass scale used in TWINSpan	14
Table 4. Number of stations by assemblage by year	17
Table 5. List of species that define each assemblage	18

LIST OF FIGURES

Figure 2-1. Chart of the Northeast Newfoundland Labrador Shelf	7
Figure 3-1. Catch-per-unit effort for each of the four assemblage areas by year	19
Figure 3-2. Composite of all stations assigned to the Deep Assemblage	20
Figure 3-3. Survey catch rates for dominant groups in the Deep Assemblage	22
Figure 3-4. Survey catch rates for less abundant groups in the Deep Assemblage	23
Figure 3-5. Composite of all stations assigned to the North Assemblage	24
Figure 3-6. Survey catch rates for dominant groups in the North Assemblage	25
Figure 3-7. Survey catch rates for less abundant groups in the North Assemblage	27
Figure 3-8. Composite of all stations assigned to the Main Assemblage	28
Figure 3-9. Survey catch rates for dominant groups in the Main Assemblage	30
Figure 3-10. Survey catch rates for less abundant groups in the Main Assemblage	31
Figure 3-11. Composite of all stations assigned to the Coastal Assemblage	32
Figure 3-12. Survey catch rates for dominant groups in the Coastal Assemblage	34

Figure 3-13. Survey catch rates for less abundant groups in the Coastal Assemblage	35
Figure 3-14. The Labrador Current system and its relation to the Newfoundland area	36
Figure 4-1. Approximate areas occupied by the four fish faunal assemblages	39
Figure 5-1. Mean bottom temperatures recorded at survey stations in each assemblage area by year	54

CHAPTER 1. FISHERIES AND FISH ASSEMBLAGES

Depletion (Hilborn and Walters, 1992) and decline of fish stocks around the world (Messiah, 1989; Frechet, 1991; Ludwig et al., 1993) in the last twenty years have pointed out the need to know the distribution of fish at diverse scales of study (Dalley and Anderson, 1993). Without such information, it will be impossible to achieve a better knowledge of the ocean's continental shelves whose ecosystems provide us with most of the world's fish resources.

The continental shelves in the Northwestern Atlantic Ocean are among the most extensive and productive areas in the world for commercial fisheries. Historically, marine fish populations have been considered too vast to be depleted by harvesting (Rosenberg et al., 1993), and this was essentially so for the Newfoundland fisheries. The result is that national and international fleets have exerted a very strong fishing effort on the stocks there for almost five centuries.

In 1977, with the extension of Canadian jurisdictional waters to two hundred miles, Canadian fisheries biologists were faced with the very difficult task of applying stock assessment procedures across the continental shelves. They had to manage the fishing grounds without having much scientific information on the fish population dynamics over a very extensive area. The size and scale of the shelf was itself a problem. The NAFO divisions 2 and 3 themselves extend over 350,000 square kilometers (Murphy and Bishop, 1993) and have a very abrupt topography and complex physical oceanography. Survey and commercial data were taken into account to set a total allowable catch (TAC) each year in order to maintain the stocks; studies were

carried out on a species by species basis. The techniques used were based on the estimation of means of total abundance and associated variances (Smith, 1990) using the standard formulae for stratified random designs (e.g. Cochran, 1977). Over the years, further improvement of the parameters used in the models produced better estimations (Cochran and Ellner, 1992).

To achieve a basic knowledge of the spatial and temporal distribution of the species seemed to be the first approach required to improve the existing model in order to take further management decisions (Dickie et al., 1987). Such an approach would be possible on the continental shelves of the Pacific coast of the United States and Canada where studies from a groundfish assemblage perspective have been carried out (Gabriel and Tyler, 1980), and similar studies are underway in the Norwegian Deep (Bergstad, 1990) and on the Grand Banks of Newfoundland (Gomes, 1993). But the Northeast Newfoundland and Labrador shelf, the area of the northern cod stock, has never been studied from this particular point of view and scale.

In the late 80's and beginning of the 90's a progressive decline in the abundance of the fish stocks through divisions 2J and 3K on the Newfoundland shelf suggested that groundfish species distributional changes might be at work; various possibilities such as overfishing or migration could account for the changes, but a spatial approach was necessary to characterize the distribution patterns and their dynamics. The fishing grounds off Northeast Newfoundland and Labrador coast are home to a number of kinds of fish, and groundfish are the main target of the fisheries. The lack of selectivity of some of the fishing gear used produces very diverse tows (i.e. containing a good mixture of species) so it seemed reasonable to approach the fisheries on a multispecies level; obviously, knowledge of each species' ecology is necessary too, but the two different approaches (individual and multispecies) may complement each other (Pielou, 1974) and together help to better understand the fisheries ecosystem.

Groundfish communities have been shown to be quite stable and exhibit distinctive assemblages that are generally aligned with the bottom topography. Rogers and Pikitch

(1992) detected six major groundfish assemblages off the coasts of Oregon and Washington based on consistencies in three types of analysis of the species weights; Colvocoresses and Musick (1984) found consistently five groundfish species associations on the Middle Atlantic Bight continental shelf over a 9-year period; Mahon and Smith (1989) described the distribution of the Scotian Shelf and Bay of Fundy demersal fish assemblages and found them to be stable and persistent through eighteen surveys (twelve in summer and three each in spring and fall) but having different outcomes at different cluster scales; Overholtz and Tyler (1985) found that the spatial integrity of each assemblage on Georges Bank was preserved over time in spite of changes in species richness and relative abundance; Gomes (1993) studied sixteen years of Spring surveys on the Grand Banks of Newfoundland and found groundfish assemblages which were persistent and homogeneous. The Northeast Newfoundland shelf has never been investigated in such a holistic manner (Atkinson, 1993) and to do so is one motive behind this thesis.

A fisheries biogeography of the shelf should provide a spatial description of groundfish distribution and disclose areas with homogeneous species composition and biomass that, if persistent over the years, have the potential to become the basic management zones that are of a size that is comfortable to monitor and regulate; changes in these areas ought to be detectable earlier than at the larger scale of the whole continental shelf scale. Such areas would be based on a multispecies sampling and analysis, and therefore would consider species biomass information important regardless of whether the species were commercially fished or not. Several environmental variables, such as bottom topography, depth, sediment type, latitude and bottom temperature, have been reported to be related to species area boundaries (Colvocoresses and Musick, 1984; Mahon and Smith, 1989; Gomes et al., 1992); therefore, such investigations may also disclose possible relations between the distribution patterns of assemblages and environmental gradients or variability.

For this study, the Department of Fisheries and Oceans (DFO) made available

fourteen years of Autumn groundfish sampling data, a number that encompasses the generation time of some of the most important groundfish on the shelf; it seems therefore plausible that species areas, if found over that duration of time on an annual basis, can be assumed to be quite stable. Numerous authors feel that the turnover time must be the minimum value of years sampled in order to obtain acceptable values; most studies that display stability in the fish assemblages have only been studied for 2 to 4 years without allowing natural variability to appear (Rogers and Pikitch, 1992). I have adopted the generation time as a good indicator based on Gomes' study (1993) done on the nearby Grand Banks area which is inhabited by quite similar species. Nevertheless, the results obtained from the analyses can only be indicative of the groundfish distribution relative to the catching gear used (demersal trawl) and the season of the year when the survey was done (Autumn) (Doubleday and Rivard, 1981; Pitt et al., 1981). This implies some bias since the timing of the survey cruises varied slightly from year to year and the environmental conditions in the area may have somewhat altered the general trends that fish follow in the Autumn when the main commercial species, mostly Atlantic cod, migrate offshore.

I have named the areas which I identify "fish assemblages", a term defined by Tyler et al. (1982) based solely on geographic distribution and by Underwood (1986) as a haphazard group of populations of various species that happen to be together at any place and time without taking into account trophic relationships. Among the species of an assemblage there may be, of course, important and complex interactions that are worthwhile studying. Therefore, the next appropriate step would be to try to find possible relationships among the components of the assemblage (Underwood, 1986) to see if they represent a true biological community. At first I had hoped to be able to address this matter but several circumstances kept me from achieving this complex task: firstly, the lack of time to finish it within the limits of a Master's thesis; secondly, the results obtained by Gomes et al. (1992) which showed a high degree of uncertainty in the outcomes of trophic interactions, and, finally the finding that the shelf ecosystem is

extremely complex in this area and that there are insufficient data to come to any fully conclusive results (Shelton et al. 1993, 1993).

In spite of the above hindrances, I have been able to address most of my original hypotheses using a multispecies approach. I have found that there are four groundfish assemblages whose species composition and abundance remain fairly constant. These have been described. They are present persistently over the fourteen years of study and they seem to be well-aligned to the bottom topography. During the first 9 years of the dataset, the groundfish assemblages described kept within fairly narrow geographical boundaries, but they seem to have undergone major changes during the last five years. This period, of course, was the one during which the fishery based on the Northern cod collapsed. Thus the study afforded an opportunity not only to describe and characterise the fish assemblages of a very large and important region of Canada's Atlantic continental shelf, but also to investigate the spatial and temporal dynamics of fish assemblages during the period of a major fishery collapse.

CHAPTER 2. MULTISPECIES DATA AND METHODS

2.1 Groundfish Data

The Canadian Federal Department of Fisheries and Oceans has been conducting Autumn groundfish surveys off Newfoundland and Labrador since 1977. The zone covered corresponds to sub-areas 2 and 3 of the Northwest Atlantic Fisheries Organization (NAFO) and specifically to divisions 2J and 3K (since 1978) and 3L (since 1981). The data used in this study were collected from 1978 to 1991 during the Autumn, mainly late October to early December, in the 2 divisions (2J3K) that correspond to the areas known as the Northeast Newfoundland and Labrador shelf (Fig. 1).

The research vessel R.V. *GADUS ATLANTICA* conducted the surveys during the entire 14 years; a stratified random method was used on groundfish sampling surveys with stratification by latitude, longitude and depth in the range from 100 to 1,000 metres. Sampling stations were allocated to strata according to area with all strata containing at least 2 stations. Tows were usually of 30 minutes duration at 2.5 knots with a 29-mm mesh liner used in the codend of the trawl (Atkinson, 1993). Surface temperature, bottom temperature at the end of the tow and depth of the tow (mean and maximum) were also recorded.

For each year, a two-way data matrix was constructed consisting of an entry (i,j) that represents the catch in weight of species j at station i . Species were included initially in the analysis only if their biomass comprised at least 0.05% of the total catch in that year's Autumn survey.

Screening of the complete species list was necessary for several reasons. Some

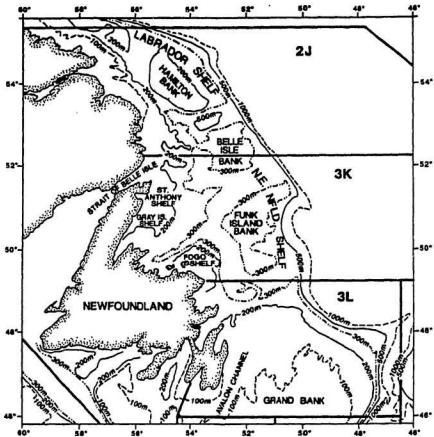


Figure 2-1. Chart of the Northeast Newfoundland and Labrador Shelf, with place names used in the text indicated. Note also NAFO Divisions 2J, 3K and 3L.

identifications were incomplete, being only done to family or genus level. Also, a number of species taken inadvertently in the demersal trawls were pelagic. Therefore, some other rules for inclusion were also established. Species were excluded if:

- 1) the data only included identification to family and with insufficient basis for species identification.
- 2) they were pelagic species, except for capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*) which play an important role in demersal food webs.
- 3) they were very large species such as Greenland shark (*Somniosus microcephalus*) or Basking shark (*Cetorhinus maximus*) which appeared very rarely in trawls but could greatly bias the analysis because of their immense weight.
- 4) their total biomass and abundance were less than 0.05% of the total fish caught in that assemblage.
- 5) they were absent more than 5 years out of the 14 sampled, except for species whose abundance or biomass was less than 0.05%, in which case the species should appear in more than 2 contiguous years.

After applying the above rules, a total of 35 species (Table 1) remained to be used in the final analyses; the number of species ranged between 28 and 35 per survey, with 29 of them (Table 2) almost always present.

Following identification of the assemblages, a further revision was done by assemblage and year to try to identify which species were most representative of the catch in each assemblage. Summaries of the basic species data finally used - by species, year, and assemblage - are found in Appendix 1.

TABLE 1: List of species used in the analysis of groundfish surveys.

Common name	Scientific name
Alligatorfish, Northern	<i>Agonus decagonus</i>
Capelin	<i>Mallotus villosus</i>
Cod, Arctic	<i>Boreogadus saida</i>
Cod, Atlantic	<i>Gadus morhua</i>
Cod, Greenland	<i>Gadus ogac</i>
Dogfish, Black	<i>Centroscyllium fabricii</i>
Eel, Longnose	<i>Synaphobranchus kaupi</i>
Eelpout, Arctic	<i>Lycodes reticulatus</i>
Eelpoui, Esmarck's	<i>Lycodes esmarki</i>
Eelpout, Vahl's	<i>Lycodes vahliei</i>
Grenadier, Roughhead	<i>Macrourus berglax</i>
Grenadier, Roughnose	<i>Trachyrhynchus murrayi</i>
Grenadier, Roundnose	<i>Coryphaenoides rupestris</i>
Flounder, Witch	<i>Glyptocephalus cynoglossus</i>
Hake, Blue	<i>Antimora rostrata</i>
Halibut, Atlantic	<i>Hippoglossus hippoglossus</i>
Halibut, Greenland	<i>Reinhardtius hippoglossoides</i>
Lumpfish, Common	<i>Cyclopterus lumpus</i>
Lumpfish, Spiny	<i>Eumicrotremus spinosus</i>
Marlin Spike, Common	<i>Nezumia bairdii</i>
Plaice, American	<i>Hippoglossoides platessoides</i>
Redfish, Deep Water	<i>Sebastes mentella</i>
Redfish, Golden	<i>Sebastes marinus</i>
Sea Raven	<i>Hemirhamphus americanus</i>
Sculpin, Arctic Deepsea	<i>Cottunculus microps</i>
Sculpin, Arctic Hookear	<i>Artediellus uncinatus</i>
Sculpin, Moustache	<i>Triglops murrayi</i>
Sculpin, Shorthorn	<i>Myoxocephalus scorpius</i>
Skate, Smooth	<i>Raja senta</i>
Skate, Spinytail	<i>Raja spinicauda</i>
Skate, Thorny	<i>Raja radiata</i>
Tapirfish, Large Scale	<i>Notacanthus chemnitzii</i>
Wolfish, Broadhead	<i>Anarhichas denticulatus</i>
Wolfish, Spotted	<i>Anarhichas minor</i>
Wolfish, Striped	<i>Anarhichas lupus</i>

TABLE 2: Species listed in Table 1, with the number of times that the species appeared during the years under study and the years when the species was absent indicated.

Scientific name	Number of years	Not present in
<i>Agonus decagonus</i>	14	-
<i>Anarhichas denticulatus</i>	14	-
<i>Anarhichas minor</i>	14	-
<i>Anarhichas lupus</i>	14	-
<i>Antimora rostrata</i>	13	78
<i>Artedius uncinatus</i>	11	81,82,83
<i>Boreogadus saida</i>	14	-
<i>Centroscyllium fabricii</i>	13	78
<i>Coryphaenoides rupestris</i>	13	78
<i>Cottunculus microps</i>	12	81,83
<i>Cyclopterus lumpus</i>	14	-
<i>Eumicrotremus spinosus</i>	14	-
<i>Gadus morhua</i>	14	-
<i>Gadus ogac</i>	10	86,88,90,91
<i>Glyptocephalus cynoglossus</i>	14	-
<i>Hemirhamphus americanus</i>	6	78-81,83-85,90
<i>Hippoglossoides platessoides</i>	14	-
<i>Hippoglossus hippoglossus</i>	13	90
<i>Lycodes esmarki</i>	10	82,83,85,86
<i>Lycodes reticulatus</i>	14	-
<i>Lycodes vahliei</i>	14	-
<i>Macrourus berglax</i>	14	-
<i>Mallotus villosus</i>	13	78
<i>Myoxocephalus scorpius</i>	10	80,81,85,87
<i>Nezumia bairdi</i>	14	-
<i>Notacanthus chemnitzii</i>	12	78,81
<i>Raja radiata</i>	14	-
<i>Raja senta</i>	14	-
<i>Raja spinicauda</i>	14	-
<i>Reinhardtius hippoglossoides</i>	14	-
<i>Sebastes marinus</i>	14	-
<i>Sebastes mentella</i>	14	-
<i>Synphobranchius kaupii</i>	12	78,81
<i>Trachyrhynchus murrayi</i>	6	78-82,84,85,89
<i>Triglops murrayi</i>	13	86

2.2 Methods

For every Autumn survey there was a log-transformation of the raw catch data of species j at station i to avoid having the most abundant species dominate the results of the multivariate analysis. Previous experience with groundfish data (Gauch, 1982; Gomes, 1987) indicated that the logarithmic transformation $\ln(1+x)$ did not change the outcome significantly as compared to the raw data analysis.

Ordination was used to represent catch and species relationships in a low-dimensional space (Gauch and Whittaker, 1981) and hierarchical classification was used to place catches into groups (Pielou, 1984). There are 2 types of hierarchical classification: *Agglomerative* classification begins with individual hauls and progressively combines them, and *Divisive* classification begins with all the hauls and progressively divides them. Ecologists have defended the practical and theoretical advantages of using polythetic divisive methods as opposed to agglomerative ones (Boesch, 1977; Gauch and Whittaker, 1981; Gauch, 1982). The later have theoretical advantages in that all the available information is used to make the critical topmost divisions, resulting in a classification that is less sensitive to influence by the random "noise" commonly found in ecological samples (Lambert et al., 1973 cited in Gomes, 1993).

Hill et al. (1975) proposed a polythetic divisive method based on an ordination technique under the name of "indicator species analysis". This method has been refined and computerized by Hill (1979) as TWINSpan; the software is designed to construct two-way ordered tables and the method of doing so is by identification of differential species. A differential species is defined as one with clear ecological preferences, so that its presence can be used to identify particular environmental conditions.

The aim of TWINSpan analysis is to throw the salient features of the data into sharp relief, by grouping like species with like, and like samples with like. Stations are classified first and the species are classified second according to their ecological preferences, using the classification of the stations as a basis. The basic steps of a TWINSpan analysis are:

- 1.- Classify the stations in a divisive hierarchy, dividing them first into 2 subsets, then 4, 8, 16, etc.
- 2.- Convert the station classification into an ordering or a rank.
- 3.- Using the groups of stations as a basis, construct attributes for the species, i.e. "preferential to the right side of the major division", "preferential the left side of the second division", etc..
- 4.- Classify the species in the same way as the stations, but with the difference that whereas the species were treated as attributes of the stations, the species have attributes of the kind indicated above in step 3.
- 5.- Convert the species classification into an ordering or a rank.
- 6.- Print out the resulting ordered two-way table, with stations as columns and species as rows.

The basic activity of TWINSpan is to make a dichotomy. The program divides up the stations into groups by repeated dichotomization, and does the same for the species. TWINSpan makes its dichotomies in a manner broadly similar to that described by Mueller-Dombois and Ellenberg (1974). They recommended dividing the species into three categories, preferential to the left, preferential to the right and those that are indifferent. Mainly because it can be argued that dichotomies do not arise naturally, these categories are nearly as arbitrary as dividing the species in two (preferential to the left and to the right as in TWINSpan), since indifference and preferentiality are a matter of degree. The stages of creating a dichotomy in TWINSpan are as follows:

- 1.- Identify a direction of variation in the data by ordinating the samples. This is referred to as "primary" ordination and is made by the method of reciprocal averaging (Hill, 1973).
- 2.- Divide the ordination at its middle to get a crude dichotomy of the samples.

- 3.- Identify differential species that are preferential to one side or the other of the crude dichotomy.
- 4.- Construct an improved ordination, referred to as a "refined" ordination, using the differential species as a basis.
- 5.- Divide the refined ordination at an appropriate point to derive the desired dichotomy.
- 6.- Construct a simplified ordination, the "indicator" ordination, based on a few of the most highly preferential species, and see whether the dichotomy suggested by the refined ordination can be reproduced by a division of the indicator ordination.

With the exception of borderline cases, the refined ordination is used to determine the dichotomy. TWINSpan introduces also the term "pseudospecies" in order to account for different "levels" of abundance or biomass in the samples.

The idea of the differential species mentioned in stage 3 is essentially qualitative, but to be effective with quantitative data it must be replaced by a quantitative equivalent. This equivalent is called a "pseudospecies" (Hill et al., 1975; Hill, 1977). The essential idea is that much of the quantitative information can be retained by expressing it on a relatively crude scale such as the Braun-Blanquet scale of cover-abundance (Mueller-Dombois and Ellenberg, 1974; Westhoff and Maarel, 1973). The levels of abundance used in TWINSpan to define the crude scale are here termed "pseudospecies cut levels".

In this study I examined fish catches and therefore a biomass scale was constructed. In order to introduce the values into TWINSpan, six pseudospecies cut levels were used based on a biomass scale covering the available data (Table 3). The values of the cut levels (0.5, 5, 25, 125, 625 and 1200) were converted into logarithms (by $\ln(1+x)$) to be comparable with the contents of the data in the input matrix.

The number of pseudospecies cut levels should represent a compromise between the *a priori* obtainable information from the data and the availability of computer space and time since each pseudospecies is stored separately in the computer. The method of pseudospecies allows quantitative values to be used as differential "species" and as

indicators. Thus, we will not have Atlantic Cod (*Gadus morhua*) as a differential species, having instead Cod1 if the biomass is higher than 0.5 kg), Cod2 if it is greater than 5 too, Cod3 if is greater than 25 and so on as differential species.

Table 3: Biomass scale with cut levels used in TWINSpan in this study.

BIOMASS RANGE (KG)	CUT LEVEL
0.5 - 5.0	0.40
5.0 - 25.0	1.79
25.0 - 125.0	3.26
125.0 - 625.0	4.84
625.0 - 1200.0	6.44
> 1200.0	7.09

As an example, following the scale shown in Table 3, imagine that station 1 has a catch of 500 kg of cod (*Gadus morhua*) whereas in station 2 only 100 kg of cod were taken. These values differ by a factor of 5 but with an application of the cut levels used in this analysis, the following pseudospecies will be present in the stations:

STATION 1 (500 kg): Cod1 (0.40), Cod2 (1.79), Cod3 (3.26) and Cod4 (4.84) showing therefore 4 pseudospecies within the single species cod.

STATION 2 (100 kg): Cod1 (0.40), Cod2 (1.79) and Cod3 (3.26) having 3 pseudospecies which in fact are in common with the 3 present in station 1.

In spite of the difference in weight (5 to 1), the stations are registered by TWINSpan as having more in common than they do by way of difference.

The final results of TWINSpan are displayed in a two-way table that fulfils requirements of non-exclusivity. An ubiquitous species can therefore be associated with more than one grouping of stations by simple visual inspection. Cluster analysis (CLUSTAN: Bray-Curtis index, Group Average method) was also used for the years 1978, 1979 and 1980; examination of the TWINSpan two-way tables allowed the recognition of biological features of each of the main station groups first identified by this cluster analysis. Such features included not only the differential species (i.e. species having clear preference for a given cluster) but also the presence or absence of a very widespread species in a cluster, or anomalies in cluster richness (number of species present). These characteristics are used to classify stations laid off the main clusters or to ratify the classification of those ambiguous stations usually located on geographical boundaries of the areas occupied by the main station groups. The use of TWINSpan allowed the derivation of more information from the data than did the cluster analysis, and for data from 1981 onwards TWINSpan was used to allocate stations to fish assemblages.

Once the two-way table produced by TWINSpan for each year was analyzed in detail, stations were assigned to the assemblages of species shown by the results. Geographical continuity was checked and the data were mapped using SIGMA PLOT and SPANS (GIS).

CHAPTER 3. CHARACTERISATION OF FISH ASSEMBLAGES

3.1 Results of the Multispecies Analyses

The TWINSpan analysis of the 14-year series of biomass survey data, comprising in all 3,520 trawl stations, identified 4 different assemblages (Deep, North, Main and Coastal) that appeared to recur regularly in the area (Table 4). Each assemblage was characterized by its own species composition and abundances; nonetheless, a number of ubiquitous species appeared in several of the assemblage descriptions (Table 5).

It was necessary to distinguish two different periods over the time course of the investigation. During the first 9 years (from 1978 to 1986), the assemblages tend to occupy the same geographic area with slight differences among the years so that a mean situation could be identified (see Fig. 4-1). Starting in 1987 and continuing until the last year in the data series (1991), the geographic position of the assemblages changed drastically and it was not possible to describe any mean spatial distribution for them any more. The areas occupied by one assemblage had been "invaded" by another assemblage which had extended beyond its mean distribution as found in the first period (1978-86); other assemblages had "shrunk" in respect to the spatial area they occupy, and, in particular zones, certain assemblages had even lost some of their main component species.

With respect to the catch per unit effort (CPUE), the most productive assemblage was the Deep one with a mean CPUE for all the species of 330 kg/tow (s.e. 45) showing its maximum in 1981 with 678 kg/tow and minimum in 1989 with 115 kg/tow; the least

productive was the Coastal one with a mean of 96 kg/tow (s.e. 15) exhibiting 219 kg/tow in 1978 and 4 kg/tow in 1991 as its highest and lowest values. The Main and North Assemblages had intermediate CPUEs of 281 kg/tow (s.e.26) and 265 kg/tow (s.e. 34) with maxima of 571 kg/tow in 1983 and 439 kg/tow in 1986 and minima of 180 kg/tow and 19 kg/tow, respectively (Fig. 3-1).

TABLE 4: Number of stations by assemblage and year for the period of study, 1978-1991; in brackets percentage of stations assigned to each assemblage within each year. Last row shows the total number of stations by assemblage for the entire 14 years.

ASSEMBLAGE YEAR	DEEP	NORTH	MAIN	COASTAL
1978	7 (5.6)	42(33.6)	67(53.6)	9(7.2)
1979	34(16.1)	54(25.6)	119(56.4)	4(1.9)
1980	42(17.6)	66(27.6)	111(46.4)	20(8.4)
1981	42(18.8)	65(29.0)	95(42.4)	22(9.8)
1982	55(18.2)	74(24.4)	134(44.2)	40(13.2)
1983	30(11.7)	84(32.8)	117(45.7)	25(9.8)
1984	36(13.7)	41(15.6)	134(51.2)	51(19.5)
1985	50(15.3)	79(24.2)	131(40.2)	66(20.3)
1986	21 (9.8)	55(25.6)	95(44.2)	44(20.4)
1987	26 (9.0)	72(25.0)	115(39.9)	75(26.1)
1988	21 (8.8)	73(30.6)	83(34.7)	62(25.9)
1989	14 (5.1)	61(22.1)	118(42.7)	83(30.1)
1990	20 (8.2)	33(13.6)	84(34.6)	106(43.6)
1991	24 (7.7)	50(16.0)	108(34.5)	131(41.8)
TOTAL #	422	849	1,511	738

TABLE 5: List of species that define each assemblage according to presence and catch per unit effort.

ASSEMBLAGE CPUE (kg/tow)	DEEP	NORTH	MAIN	COASTAL
> 100	Deepwater Redfish	Atlantic Cod	Atlantic Cod Deepwater Redfish	----
10 -100	Greenland Halibut Roundnose Grenadier Broadhead Wolffish	American Plaice Broadhead Wolffish Greenland Halibut	Greenland Halibut	Atlantic Cod Greenland Halibut American Plaice
1 - 10	Roughhead Grenadier Black Dogfish	Spotted Wolffish Striped Wolffish Thorny Skate Roughhead Grenadier	Golden Redfish American Plaice Witch Flounder Broadhead Wolffish	Thorny Skate.
< 1	Blue Hake Marlin Spike	Witch Flounder Arctic Cod	Striped Wolffish Arctic Eelpout Spotted Wolffish Arctic Cod	Arctic Cod, Witch Flounder Arctic Eelpout

There seemed to be a good correspondence between the distribution of the assemblages and the bottom topography of the area. The NE Newfoundland and Labrador shelves (NAFO Divisions 2J and 3K) are very profuse in banks (Harrison,

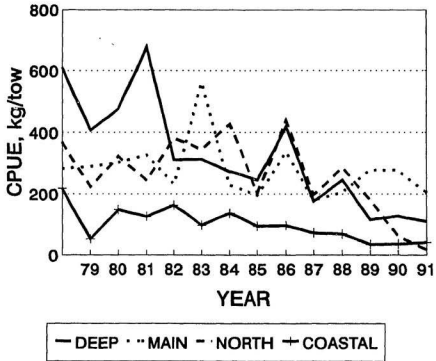


Figure 3-1. Catch-per-unit effort (kg/tow, all species) for each of the four assemblage areas by year.

Hamilton, Belle Isle, Funk Island), saddles (Cartwright, Hawke), basins (e.g. St. Anthony) and deeps (e.g. Funk Island). This correspondence agrees with the literature on fish assemblages mentioned in Chapter 1, and seems to be a common finding in all studies done on the matter.

3.1.1 DEEP ASSEMBLAGE

3.1.1.1 Description and Environmental conditions

As the name indicates, stations that belonged to this assemblage were situated in the deeper areas of the Northeast Newfoundland and Labrador shelves (Fig. 3-2). The assemblage occupied an elongated area in both NAFO Divisions 2J and 3K located along the shelf-slope break at latitudes ranging from 55°30'N to 49°30'N and longitudes from 55°30'W to 50°W. The Deep Assemblage was the only one that maintained its spatial distribution during the entire 14 years of study, and also showed certain stability and little variation in the environmental variables studied.

The number of stations assigned to the Deep Assemblage ranged from 7 in 1978 to 55 in 1982 with a mean of 30 (SD=13) stations per year. From 1978 until 1982 there was an increasing number of stations surveyed that showed

characteristics of the Deep Assemblage, but from 1982 to 1989 the number decreased dramatically only increasing slightly to 24 stations in the assemblage in 1991. The mean depth fluctuated between 688 ± 39 metres (SE) in 1991 and 349 ± 17 m in 1978; 1334 m in 1979 was the deepest station surveyed during the 14 years and 231 m in 1982 was the shallowest. The greatest range in any one year was in 1979 with stations at depths between 1334 and 233 m.

The mean bottom temperatures were the warmest values of all the assemblages with temperature means from $4.18 \pm 0.29^\circ\text{C}$ (SD) in 1983 to $2.66 \pm 1.21^\circ\text{C}$ in 1979,

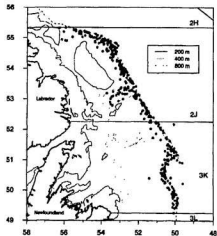


Figure 3-2. Composite of all stations assigned to the Deep Assemblage, 1978-1991

reflecting the quite stable bottom temperature in this area. The warmest individual station was found in 1991 (5.1°C) and the colder ones showed a temperature of 0°C in different years. In 1983, 1988 and 1989 the mean bottom temperature was warmer than average, and 1980 and 1984 were colder years.

Mean surface temperature in the area of the Deep Assemblage was calculated even though it probably should not be considered very important as regards groundfish analysis. Values ranged from $2.97 \pm 1.24^\circ\text{C}$ (SD) in 1980 to 0°C (SD=0) in 1991 with the warmest individual station surveyed in 1979 (7.0°C) and the coldest in 1984 (-1.2°C). The years 1978, 1984 and 1989 exhibited cooler than average temperatures whereas 1979, 1980 and 1988 were warmer.

3.1.1.2 Biomass and Species Composition

The catch per unit effort of this assemblage exhibited a decreasing trend from 1978 to 1991. In certain years, the CPUE appeared to increase but this was due to *Sebastes* species (mainly *Sebastes mentella*) which were occasionally taken in enormous quantities (order of 11 tons) in some tows especially in 1983, 1986 and 1988. Excluding these unusual redfish tows, CPUE in the Deep Assemblage had a decline of 500 kg/tow in 14 years varying between 610 kg/tow in 1978 and 110 kg/tow in 1991 with a mean of 330 ± 46 kg/tow (SE). This assemblage exhibited a bigger decrease than the others, but this could be due to the high natural variation in the catchability that characterised the deepwater redfish (*Sebastes mentella*), a dominant species. The mean CPUE of the whole assemblage showed no significant difference among years, with the exception of the strong redfish year 1981; when the unusual tows of redfish were removed, any difference disappeared.

Deepwater redfish (*Sebastes mentella*) was the most abundant species with CPUE values greater than 100 kg per tow. Greenland halibut (*Reinhardtius hippoglossoides*) was the next most abundant species with CPUEs that were between 20 kg per tow in 1989 and 100 kg per tow in 1986, when it comprised 25% of the total catch in the

Dominant species - Deep Assemblage

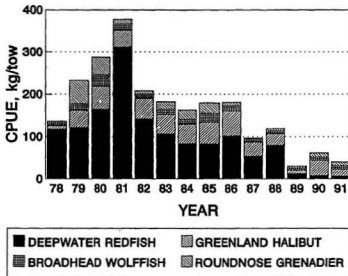


Figure 3-3. Survey catch rates for dominant (and commercial) groups in the Deep Assemblage.

assemblage (Fig. 3-3).

Broadhead wolffish (*Anarhichas denticulatus*) was a very important species in the Deep Assemblage too, showing a CPUE between 10 and 40 kg per tow; it was most abundant in 1978 and 1980. At about the same level of abundance and characteristic of this assemblage in considerable amounts was the roundnose grenadier (*Coryphaenoides rupestris*), with CPUE ranging from 20 to 70 kg per tow (Fig. 3-3).

Roughhead grenadier (*Macrourus berglax*) and black dogfish (*Centroscyllium fabricii*) were an order of magnitude less abundant in the Deep Assemblage with CPUEs ranging from 4 to 15 kg per tow (Fig. 3-4). Blue hake (*Antimora rostrata*) and marlin spike (*Nezumia bairdii*) were always present in this assemblage but in very small

Less abundant species - Deep Assemblage

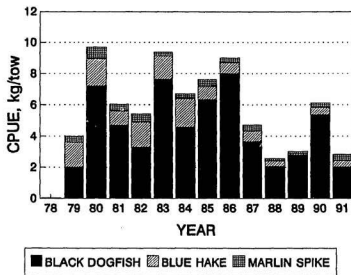


Figure 3-4. Survey catch rates for less abundant (and non-commercial) groups in the Deep Assemblage.

quantities, i.e. less than 1 kg per tow during all 14 years.

3.1.2 NORTH ASSEMBLAGE

3.1.2.1 Description and Environmental conditions

The North Assemblage occupies mainly NAFO Division 2J but in some years extends southward into 3K (Fig. 3-5). It comprises a narrow area north of the Main Assemblage and to the east of the Coastal Assemblage. From 1978 to 1987 it lies within the latitudes from 50°45'N to 55°30'N and longitudes between 57°30'W to 53°W; after 1987, the assemblage shifted slightly towards the north and east to latitudes between 51°10'N and 55°30'N in 1987, 1988 and 1989 but between 53°15'N and 55°30'N in

1990 and 1991 and longitudes between 56°12'W and 52°25'W in all these five years.

A mean of 60 (SD=15) stations per year were found to fall within this assemblage. The lowest number of stations in any one year was 33 (in 1990) and the highest was 84 (in 1983). In general, the North Assemblage includes an increasing number of stations from 1978 to 1983; in 1984 there was a sharp decrease and from that year it decreases erratically until 1990. There was some recovery in 1991 when 50 stations were found with the characteristics of the North Assemblage.

The mean depth sampled ranges from 210 ± 49 m (SD) in 1982 to 296 ± 112 m in 1991, with the shallowest individual station depth measured in 1981 (104 m) and the deepest in 1991 (835 m). The North Assemblage had mean bottom temperatures ranging from $0.02 \pm 0.83^\circ\text{C}$ (SD) in 1984 to $1.92 \pm 0.95^\circ\text{C}$ in 1988; the warmest stations recorded were in 1978 and 1981, registering 4.5°C , and the coldest measured was in 1984 (-1.2°C). As a trend, the mean bottom temperature in this assemblage decreased from 1978 to 1984, increased from 1984 to 1986, diminished in 1987 and then increased slightly until 1991.

Mean surface temperature for North Assemblage stations ranges from $-0.24 \pm 1.03^\circ\text{C}$ (SD) in 1984 to $1.55 \pm 1.71^\circ\text{C}$ in 1979. The coldest station registered was in 1984, having a surface temperature of -1.9°C , and the warmest was in 1979 with 6.4°C . The data show two peaks characterized by an increase followed by a decline in

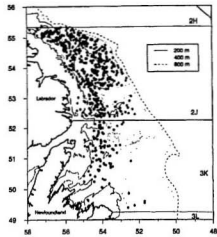


Figure 3-5. Composite of all stations assigned to the North Assemblage, 1978-1991.

Dominant species - North Assemblage

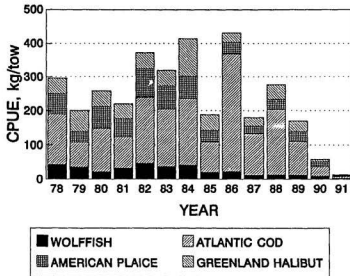


Figure 3-6. Survey catch rates for dominant (and commercial) groups in the North Assemblage.

the surface temperature. The warmest years were 1979, 1980, 1982 and 1985 whereas the coolest were 1978, 1984 and 1991.

3.1.2.2 Biomass and Species composition

The CPUE in the North Assemblage ranged from 438.6 kg/tow in 1986 to 18.58 kg/tow in 1991. A massive decline was detected in 1990 and 1991 when less than 50 kg/tow were taken as compared with the mean overall of 265 ± 34 kg/tow (SE). The catch was 400 kg/tow in 1978, decreased to 250 kg/tow in 1981, and then increased progressively until 1986 where 438.6 kg/tow were taken. From 1986 onwards, the catch per unit effort decreased sharply showing a CPUE of only 18.58 kg/tow in 1991.

Atlantic cod (*Gadus morhua*) is one of the principal species within this assemblage until 1989 (a mean of about 150 kg/tow). From 1989 the CPUE for this species shows a declining trend to arrive at nearly 0 kg/tow in 1990 and 1991 (Fig. 3-6). It comprises a high percentage of the total in the catches for the North Assemblage (around 50% before 1989 and 30% thereafter).

Greenland halibut (*Reinhardtius hippoglossoides*) showed a CPUE of about 40 kg/tow until 1988, with the exception of 1984 when a mean of 110 kg/tow was taken. From 1988 onwards a sharp decrease was found with values of less than 10 kg/tow in 1990 and 1991. Nevertheless the percentage in each year's catch of Greenland halibut within the North Assemblage remained mostly around 20%. American plaice (*Hippoglossoides platessoides*) was another of the important species in this assemblage. It showed values of CPUE around 60 kg/tow until 1984 but these decreased to 2 kg/tow in 1991. However, as with the Greenland halibut, the percentage comprised by plaice over the years remained very stable around 15%.

Deepwater redfish (*Sebastes mentella*) was another North Assemblage species that showed a decreasing trend in the catch, especially from 1988 onwards. But, as was mentioned above, redfish appeared very erratically and, though 60 kg/tow were caught in 1978, the general trend showed a mean of 10 kg/tow until 1987 and redfish were nearly completely absent from 1988 until 1991. Broadhead wolffish (*Anarhichas denticulatus*) showed the same as the other species that predominated in this assemblage - a declining trend from 1984 onwards (Fig. 3-7) but again with the percentage within the total catch every year quite constant around 8%. CPUE for this large wolffish species was around 25 kg/tow until 1984 and about 8 kg/tow from 1985 from then on until the last year of the study when only 2 kg/tow were caught.

Spotted wolffish (*Anarhichas minor*) and striped wolffish (*Anarhichas lupus*) were species that appear in the North Assemblage but in lower percentages, about 3% of the total catch for the year; in 1991, a slight increase was noticeable in both species, amounting to 5% and 10% respectively of the total biomass caught. Thorny skate (*Raja*

Less abundant species - North Assemblage

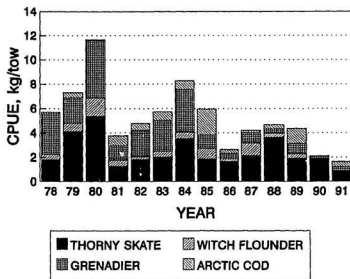


Figure 3-7. Survey catch rates for less abundant (and non-commercial) groups in the North Assemblage.

radiata) and roughhead grenadier (*Macrourus berglax*) are North Assemblage species with a CPUE of about 3 kg/tow. Arctic celpout (*Lycodes reticulatus*), witch flounder (*Glyptocephalus cynoglossus*) and Arctic cod (*Boreogadus saida*) represented only around 1 kg/tow of the total catch of the assemblage each year.

3.1.3 MAIN ASSEMBLAGE

3.1.3.1 Description and Environmental conditions

The Main Assemblage was the principal assemblage in respect to the extent of area occupied and the number of stations sampled each year (Fig. 3-8). From 1978 to 1986, the assemblage was located at latitudes between 53°30'N and 49°30'N and

longitudes from 54°W to 50°30'W. Beginning in 1987 and continuing thereafter its extent shrank to occupy longitudes only between 53°24'W and 50°W. At the same time, there began to appear areas within this assemblage that had characteristics of the Coastal Assemblage (see below). These "holes" were localized at longitudes from 51° to 53°W and latitudes between 52° and 52°30' N, 50°30' and 51°30'N and 49°30' and 50°N. The result was that the Main Assemblage came to cover a smaller area.

There was a mean of 108 (SD=20) stations per year within the Main Assemblage, with the minimum of 67 stations occurring in 1978 and a maximum of 134 in both 1982 and 1984. The shallowest mean depth of the stations that belong to the Main Assemblage was 287 m in 1978 and the deepest was 382 metres in 1990. For individual stations, the shallowest was in 1978 (191 m) and the deepest sampled was 863 m in 1990. The greatest depth range was in 1990 (222-863m, 84 stations) and the least was found in 1978 (202-400m, 67 stations).

The mean bottom temperature ranged from 1.75°C in 1985 to 3.11°C in 1980, with the greatest scope in 1983 (0.9-5.8°C). There was a general decrease in mean bottom temperature from 1978 to 1985 from 3.1°C to 1.75°C and then a gradual increase to 3.09°C in 1991. Mean surface temperature ranged from 0°C in 1991 to 3.11°C in 1980, with a slightly increasing trend from 1978 (2.19°C) to 1980 (3.11°C). From 1980 on there was a general decrease with some ups and downs to end up at 0°C

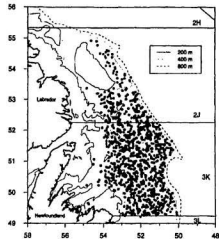


Figure 3-8. Composite of all stations assigned to the Main Assemblage, 1978-1991.

in 1991 due to the freezing conditions. The highest surface temperature ranges were found in 1979, 1980 and 1982 with ranges of 7.4, 7.0 and 6.0°C respectively; for individual stations, 7.2°C (1980) was the warmest encountered in this area in all years while -1.0°C was the coldest and recorded in 1979.

3.1.3.2 Biomass and Species Composition

The Main Assemblage, by its characteristic species composition as well as by its mean depth of the stations, resembled very much the NES Deep Assemblage described by Gomes (1993) for the Grand Banks of Newfoundland. This appreciation was obvious because the Main Assemblage could be described as a prolongation to the north of Gomes' assemblage (fish do not know about the NAFO areas!) with slight differences in the relative abundance of certain species. The Main Assemblage was limited to the east by the Deep Assemblage whose border seemed to mark the approximate limits of distribution of Atlantic cod, American plaice and witch flounder. Deepwater redfish increased in relative importance when moving from the Main to the Deep Assemblage to the east. The Main Assemblage was limited by the North Assemblage to the north and northwest and by the Coastal Assemblage to the west.

Atlantic cod was the most abundant species in the Main Assemblage (Fig. 3-9) with a mean CPUE of 140 kg/tow over all years. There seemed to be a general decreasing trend from 1978 (100 kg/tow) to 1988 (50 kg/tow) but in 1986 there is some recovery (170 kg/tow) that continues in 1989, 1990 and 1991 (160 kg/tow). At the beginning of the study series, this species represented about 35% in weight of the total catch but by the last years it had become most of the catch (78% in 1991). This fact probably resulted from the disappearance of many less abundant species, especially from certain areas as was mentioned earlier (sec. 3.1).

Deepwater redfish in the Main Assemblage exhibited a very high CPUE between 1978 and 1981 with a mean of about 425 kg/tow. The value dropped to 125 kg/tow between 1982 and 1988 and ended up at only 10 kg/tow from 1989 to 1991. Deepwater

Dominant species - Main Assemblage

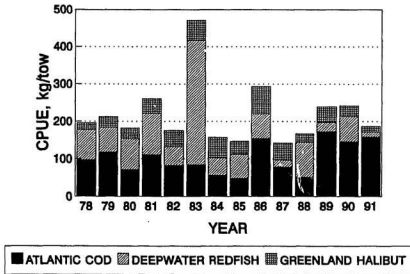


Figure 3-9. Survey catch rates for dominant (and commercial) species in the Main Assemblage.

redfish represented on average about 30% in weight of the total catch over all years, with exceptions in 1983 (60%) and 1988 (45%) which were in keeping with the interannual variability characteristic of this species. Greenland halibut CPUE showed an increasing trend from 1978 when 20 kg/tow were taken to 1986 with 75 kg/tow. From 1987, however, the species started to decline in abundance to reach an average of 15 kg/tow during the rest of the period of study. Greenland halibut represented about 15% in weight of the total catch over the years. Golden redfish exhibited an abundance of 50 kg/tow in 1980 and 30 kg/tow in 1983, but from 1984 on declined sharply to 5 kg/tow (it should be emphasized that the identification of this species may not be very satisfactory due to its similarity with the Deepwater redfish; in some cases this difficulty

results in both species being classified under the generic "Redfish spp.).

American plaice and witch flounder were species that displayed a very similar behaviour throughout all years in this assemblage (Fig. 3-10). Both species were present in the samples with a CPUE around 20 kg/tow in 1978 (21 and 17 kg/tow respectively), both showed a declining trend until 1991 where they only were caught in values of 5 and 2 kg/tow, and both represented a mean of 7% in weight of the total catch by year. Broadhead wolffish shows the same decline as these two species; it had a CPUE of 14 kg/tow in 1978 while in 1991 its presence was barely 2 kg/tow. This species comprised 5% of the total weight in the Main Assemblage over the years of study.

Less abundant species - Main Assemblage

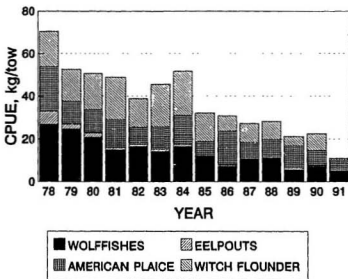


Figure 3-10. Survey catch rates for less abundant (usually non-commercial) species in the Main Assemblage.

Thorny skate and roughhead grenadier were present at a lower order of magnitude (Fig. 3-10), representing only around 5 kg/tow in 1978 and decreasing to 2 kg/tow in the former and to 1 kg/tow in the latter. These species comprised only 2% of the weight of the total catch over the years. Other species that appeared in very low abundance were striped wolffish, Arctic eelpout, spotted wolffish and Arctic cod in descending order of abundance.

3.1.4 COASTAL ASSEMBLAGE

3.1.4.1 Description and Environmental conditions

The Coastal Assemblage had its eastern border with the North Assemblage in the north and the Main Assemblage in the south (Fig. 3-11). It had the lowest species diversity of any assemblage, and seemed to be associated with the inshore colder branch of the Labrador current. The Coastal Assemblage did not appear conspicuously every year, for example as in 1979, but in other years it occupies an area even larger than that of the Main Assemblage itself, for example as in 1984. The primary difference between this assemblage and the Main Assemblage, apart from the low abundance and diversity, was the absence of all the wolffishes (Broadhead, spotted and striped). The Coastal Assemblage covered an elongate area along the coast in NAFO Divisions 2J and 3K between latitudes 49°30'N to 55°30'N during all 14 years of the study; from 1978 to 1986 it fell

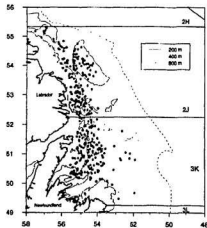


Figure 3-11. Composite of all stations assigned to the Coastal Assemblage, 1978-1991.

on average between longitudes 53°30'W to 57°30'W, but from 1987 to 1991 it extended its stations to the east to longitudes ranging from 52°30'W to 57°30'W and occupying the "holes" left by the shrinking of the Main Assemblage; in 1991 there were even some Coastal Assemblage stations at 51°W.

The number of stations in the Coastal Assemblage was generally lower than average until 1984 but from 1985 the number increases rapidly; there were only four stations in 1978 but there were 133 in 1991, with a mean of 53 (SD=36) stations per year. This was the shallowest assemblage with mean yearly depths between 178 m and 274 m; for an individual station the shallowest value was in 1989 at 103 m and the deepest was in 1991 at 494 m. The greatest depth range was in 1990 (116-485 m) and the least in 1979 (148-240 m).

The mean bottom temperature for the Coastal Assemblage ranged from -0.85°C in 1984 to 1.3°C in 1991 with individual station extremes of -1.9°C in 1984 and 4.1°C in 1991. This last year also had the greatest range of individual bottom temperatures with values between -0.7 and 4.1°C. The mean surface temperature ranged from 0°C in 1978, 1984 and 1991 to 1.4°C in 1981. The warmest temperature recorded was 3.9°C in 1989 and the coolest was -1.2°C measured in 1984; the greatest range was found in 1989 with surface temperatures between -0.4 and 3.9°C.

3.1.4.2 Biomass and Species Composition

Greenland halibut, Atlantic cod and American plaice were the main components of the Coastal Assemblage (Fig. 3-12). The first species showed a mean CPUE of 50 kg/tow except in 1978 when a CPUE of 125 kg/tow was recorded. The Greenland halibut CPUE declined to 10 kg/tow in 1984 and increased slightly from 1985 until 1991 where a mean of 15 kg/tow occurred; its percentage by weight stayed mostly around 20% with several years of higher catch in 1978 (57%), 1980 (45%) and 1990 (65%).

Atlantic cod was another important species in this assemblage. It had an increasing trend in catch rate from 40 kg/tow taken in 1978 to about 95 kg/tow in 1985

Dominant species - Coastal Assemblage

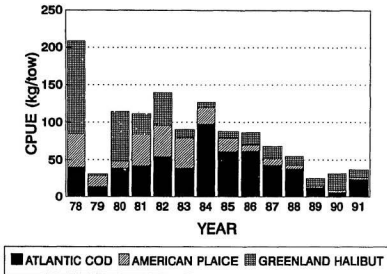


Figure 3-12. Survey catch rates for dominant (and commercial) species in the Coastal Assemblage.

and 1986. Thereafter it decreased to only 5 kg/tow in 1990 and recovered slightly in 1991 to 25 kg/tow; in spite of these changes, cod consistently represented around the 50% in weight of the species that make up the Coastal Assemblage. American plaice had a CPUE average of 40 kg/tow until 1985, but in 1986 this value was reduced significantly to 10 kg/tow and after 1987 only 4 kg/tow were taken as a mean per year. Plaice represented around 20% in weight until 1986, and from that year onward only 10% of the total catch per year was comprised by this species.

Thorny skate, Arctic eelpout, witch flounder and Arctic cod were minor species always present in the Coastal Assemblage but in very low abundance (Fig. 3-13). They all showed values of CPUE less than 3 kg/tow and represented no more than 1% in

Less abundant species - Coastal Assemblage

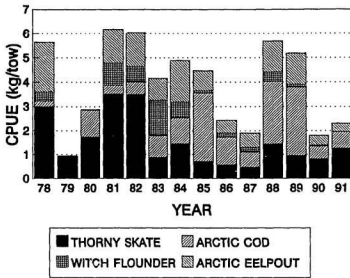


Figure 3-13. Survey catch rates for less abundant (and non-commercial) species in the Coastal Assemblage.

weight of the total species catch in any year.

3.2 Oceanography and Assemblages

The Northeast Newfoundland Shelf is one of the three major parts of Newfoundland's continental shelf, and is the widest continental shelf outside of the Arctic. It is about 300 km wide and 1500 km long, with an average depth of about 200m. Many of its numerous inshore embayments are deeper than 200m. The offshore part of the shelf presents several banks of about 300m with the basins reaching 500m in some areas (Helbig et al., 1992). The shelf is wider and shallower to the South where it forms the Grand Banks of Newfoundland and is narrower and more complex towards

the North where it constitutes the Labrador Shelf.

The Labrador Current (Fig. 3-14) dominates the Northeast Newfoundland and Labrador Shelf; it is the presence of this major current that gives the shelf its polar characteristics, with temperatures below zero and salinities around 34-35 ppt. It is composed of three different water types that meet near the northern tip of Labrador, i.e. Arctic water that comes through the Hudson Strait, Arctic water from Baffin Bay and a fraction of water from the West Greenland Current. Two distinct branches of the Labrador current are found on the Labrador Shelf: the offshore branch flows parallel to a polar front that extends along the length of the shelf and is trapped on the continental slope and getting stronger over the 600m-800m isobaths (speed of 80 cm/s) and the inshore branch which is weaker (e.g. surface speed of 10cm/s) and it is evident in the upward sloping isohalines over the shelf (Lazier, 1982; Helbig et al., 1992).

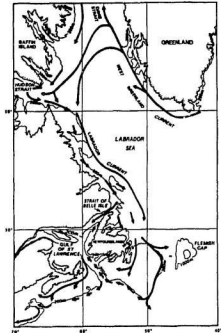


Figure 3-14. The Labrador Current system and its relation to the Newfoundland area.

When the Labrador Current reaches the Northeast Newfoundland shelf, most of the offshore branch remains bathymetrically trapped over the continental slope flowing on to the south around the Grand Banks to turn west to the north of the Gulf Stream system; the other branch remains inshore, part of it going through the Strait of Belle Isle (Petrie and Anderson, 1983) and intensifies until reaching the Avalon Channel and finally rounding the southern coast of Newfoundland (Helbig et al., 1992).

The main offshore branch of the Labrador Current carries the greatest volume of water. It is relatively warm and saline (temperature of 3 to 4°C and salinity around 34.9 ppt). It seems to be associated with the Deep Assemblage and contributes to the quite stable bottom temperatures observed there.

The Main Assemblage also seems to be associated with the Labrador Current main branch. Bottom temperatures of this assemblage are above zero though lower than found in the Deep Assemblage, probably due to the presence of the polar front.

The inshore cold and fresher branch of the Labrador Current (temperatures of -1° to 2°C and salinity of 32.5 to 33.5 ppt) can be related to the Coastal Assemblage which shows a low diversity of species; the possible changes in the extension of the inner branch during the cold years of the 80's may account for the expansion to the east of the Coastal Assemblage. The increasing presence of species quite tolerant to low temperatures, such as Arctic cod (Lilly et al., 1994) or Arctic eelpout (Fig. 3-13), in this assemblage may reflect this expansion.

The North Assemblage exhibits a mix of waters with characteristics of both branches of the Labrador Current. This is probably the case because it occupies the area of the Deep Assemblage to the north and certain areas inshore to the south which run parallel to the inner branch of the Labrador Current; nevertheless, the bottom temperature associated with this assemblage was mainly positive indicating a greater affinity to the offshore branch. The North Assemblage did not extend southwards in the last years of study, a situation which may also be due to the inshore branch expansion across the shelf.

CHAPTER 4. TEMPORAL CHANGE OF FISH ASSEMBLAGES

4.1 Mean Situation

During the first 9 years of study, the four assemblages were found in recurrent areas with slight differences from year to year presumably due to the inherent variability of the ecosystem; therefore, a general situation can be presented wherein the geographic position of the groups of stations that represent each of the fish assemblages of the Newfoundland and Labrador shelf is plotted using the data from those years (1978-1986) as representative of the most typical situation (Fig. 4-1). Persistence over time of this sort has been found by studies of fish assemblages in different oceans (Colvocoresses and Musick, 1984; Tyler et al., 1982; Overholtz and Tyler, 1985; Mahon and Smith, 1989; Rogers and Pikitch, 1992).

Starting in 1987, however, a mean picture can no longer be described for Newfoundland and Labrador, a situation which could be caused, probably, by a loss of global stability in the system; in these last five years the system seems to be changing towards a different alternative stability (Walters and Holling, 1990). Since the stability of a community depends on the environment in which it exists as well as on individual densities and species composition, the spatial variation in the fish assemblage areas could be related to physical as well as population parameters that may have changed significantly in the period beginning in 1987.

4.2 First Period: 1978-1986

Despite the fact that a mean situation has been described, anomalies appear in

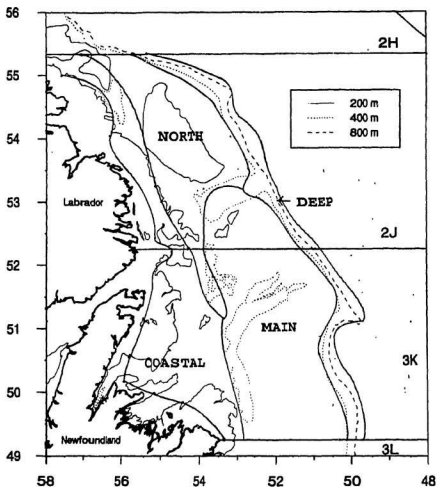


Figure 4-1. Approximate areas occupied by the four fish faunal assemblages on the Newfoundland-Labrador Shelf: Coastal, North, Main, and Deep.

the spatial distribution as well as the depth and temperature ranges for each assemblage on a year-to-year basis. The map figures show in different colours the stations that

belong to each assemblage; no attempt has been made to draw any contours. These maps should be compared to the mean situation (Fig. 4-1) where contours were drawn more to set up limits than to characterize any specific years' distribution of the assemblages. Yellow dots represent stations that belong to the so-called Deep Assemblage, red are Main stations, North Assemblage is represented by black dots and orange is used for the Coastal stations; the dot is placed in the exact latitude and longitude of the station sampled. The different blue tones of the background represent the bathymetry of the area ranging from white (0-100m) to light blue (200m) and increasingly darker blue until > 800m. The base map covers latitudes (48°N to 55°50'N) and longitudes from 49°W to 59°W including therefore NAFO areas 2J and 3K in their entirety.

Autumn 1978

This year's cruise contains the lowest number of stations, especially for the Deep and Coastal Assemblages (GIS map of 1978). It presents in general an average distribution pattern though the depth of the stations that comprise the Main group are somewhat shallower (392 m was the deepest station sampled in this group) than normal; even so it showed the general trend because the deepest station measured in the whole area was only 400 m deep. Witch flounder appears in the Deep group this year with 5 kg/tow taken, probably due to sampling in shallower stations. The CPUE of Greenland Halibut in the Coastal Assemblage has a value much greater than the mean for all the years and was the only occasion when over 100 kg of this species were caught in this group (125 kg/tow). Spotted and Striped wolffish appear at a higher CPUE than any other year in the Main group; the same occurs for the latter in the North Assemblage and for Roughhead grenadier in the Deep group. Arctic cod shows its higher abundance in the Main group in 1978 too. Colder than average surface temperature were found in the North and Coastal Assemblages.

Autumn 1979

Stations with the characteristics of the North group appeared very far south this

year, reaching latitudes of 50°30'N. The Main Assemblage extends slightly northwards appearing north of Hawke Saddle and occupying the area normally belonging to the North Assemblage. Some very deep stations were measured within the Deep Assemblage reaching 1334 m to the east of the slope break. Main and North groups exhibited very low values for Atlantic cod. No Arctic cod were found in the Coastal Assemblage. The highest CPUE for Roundnose grenadier in the Deep group over all years occurred in 1979 (72 kg/tow).

Autumn 1980

There is certain intrusion of the Deep Assemblage into the area of the North Assemblage along Cartwright Saddle with the result that the mean bottom temperature is unusually low in the Deep group. The North Assemblage extends southwards reaching the southern part of the Funk Island Deep. The other assemblages remained as in the mean situation. Golden redfish shows its peak in the Main Assemblage during this year reaching nearly 60 kg/tow; the same occurs for Roughhead grenadier in the North Assemblage but in much lower abundance. Arctic eelpout disappears this year from the assemblages whereas Broadhead wolffish reaches a maximum CPUE for all years in the Deep group; the same applies to Thorny skate in the North group. Marlin spike, a component in low abundance in the Deep group appears more abundant in 1980 than in the rest of the years.

Autumn 1981

The Coastal Assemblage appeared mainly to the south in NAFO area 3K with only 2 stations in 2J. The North group invaded the Coastal Assemblage area in 2J. Thorny skate and American plaice increased to their peak abundance in the Coastal group this year and maintained this abundance through 1982. In 1981, the highest CPUE for Deepwater redfish was found, with 430 kg/tow being caught in the Deep group.

Autumn 1982

North stations keep intruding into areas more normally Coastal, especially around latitude 53°30'N. The rest of the situation is equivalent to the mean. Colder than average bottom temperature occurred for the Coastal and North Assemblages. This is a cold surface temperature year for the Main Assemblage but is warmer than usual for the North. Highest values of abundance of American plaice, Broadhead wolffish, Spotted wolffish and Arctic eelpout in the North group over all years occur in 1982.

Autumn 1983

In contrast to 1982, it is the Coastal Assemblage that starts invading the North group area, especially on the western part of Hamilton Bank. The North Assemblage elongates southwards reaching again latitudes of 50°N, similar to the situation in the fall of 1979. Bottom temperatures were even colder for the Coastal and North Assemblages, but were the warmest encountered so far for the Deep Assemblage. Greenland halibut abundance diminished greatly to less than half that found previously in the Coastal Assemblage. Another strong peak of abundance occurs in Deepwater redfish with 340 kg/tow caught in the Main group, largely the result of two very large catches at 286 m (11,050 kg) and 344 m (11,948 kg). Striped wolffish reaches its maximum CPUE in the North group in 1983.

Autumn 1984

St. Anthony Basin and Hamilton Bank, areas that formerly had stations characteristic of the North and Main Assemblages are being taken over by the Coastal Assemblage. The North and Coastal Assemblages continued to have very low mean bottom temperatures and the Deep Assemblage appears cooler too. The surface temperature has decreased in all the groups. This year Atlantic cod shows the maximum CPUE over all years in the Coastal Assemblage and Thorny skate in the Main; furthermore, Greenland halibut in the North nearly recovers to its maximum of 125

kg/tow that was found in 1978 in the Coastal group. In the Main group, Witch flounder reaches its maximum CPUE and the less abundant Blue hake does the same in the Deep group.

Autumn 1985

The Deep Assemblage takes over Hawke Saddle reaching as far west as 53°30'W and covering an area usually occupied by species typically belonging to the Main group. The Main group also gets invaded from the north by the North group which appears south of Hawke Saddle while stations that belong to the Coastal group increase in Hamilton Bank. Temperatures in the Coastal Assemblage continue to cool off whereas in the others a normal average temperature occurs. Atlantic cod and American plaice show a lower abundance than in previous years (except 1979) in the North group. Arctic cod shows maximum CPUE peaks in the North and Coastal Assemblages this year as compared with all other years. Roughhead grenadier abundance decreases this year relative to the previous situation in the Deep and North Assemblages.

Autumn 1986

This year shows a situation very similar to the mean, although very few Deep stations were surveyed. There were more stations sampled than in 1978 but the picture in regard to the spatial distribution of assemblages is very similar. This year exhibits very cold surface temperatures in all the assemblages. There was a sudden increase of Roughhead grenadier relative to previous years (except 1978). Black dogfish, a low abundance species in the Deep group, reaches its maximum value this year. Striped wolffish features the lowest abundance as compared to previous years in the North and Main Assemblages while Spotted wolffish shows the highest abundance in the Deep group. The North Assemblage presents the highest catch of Atlantic cod in all the assemblages over all years with 350 kg/tow taken in 1986, a great increase from previous years. In the Main group, the same occurs for this species but at a lower scale of

abundance. The Deep and Main Assemblages displayed the greatest abundance of Greenland halibut over all years.

4.3 Second Period: 1987-1991

Colour maps were also made for the five years comprising this period, and should be interpreted in the same way. Now, however, comparisons with the mean are senseless because the spatial variability is enormous and it seems to have certain inherent dynamic behaviour towards increased instability. The observed anomalies are the result of three major shifts, namely that the North Assemblage is moving southwards as it did sporadically during the first period and in some cases to the east as well, the Main group is moving deeper taking over certain areas occupied previously by the Deep group, and the Coastal group is invading the Main and the North group areas to the east. The latter produces what I have called "holes", i.e. areas that in the mean situation spatially belonged to an assemblage but that were taken over by another one due to a change in species composition and abundance in the stations sampled in the area. This dynamic picture will be described on a year-by-year basis in order to trace its realization most clearly.

Autumn 1987

The Coastal group spreads east to the south of Funk Island Deep and thereby starts to produce a hole. Stations with Main composition and abundance of species appear north of Hawke Saddle between the Deep area and the 200 m isobath on the Labrador shelf. The Coastal group takes over the Hamilton Bank area and south of Hawke Saddle, the North Assemblage occupies an area usually representative of the Main group. The Coastal bottom temperature gets cooler as does the surface temperature of the Main, North and Deep Assemblages. Blue hake abundance starts to decrease in the Deep group; the same happens to Greenland halibut that diminishes to nearly half of its abundance in 1986 in the Deep and Main Assemblages. All the assemblages that include

Broadhead wolffish in their composition exhibit a sharp decrease in abundance of this species in 1987 with respect to previous years. Atlantic cod continues a decreasing trend with respect to the previous year in the North and Main Assemblages due to the sudden increase in abundance found in 1986. American plaice, Spotted wolffish and Deepwater redfish have the same reduction in abundance with respect to previous years in the North and Deep groups. Striped wolffish decline in the Main and North groups; Arctic cod and Arctic celpout do the same in the Coastal and North Assemblages. Roundnose grenadier has its lowest abundance over all years of study in 1987; no Golden redfish were caught this year.

Autumn 1988

The Main group is not so much distributed to the north, but does keep invading areas usually occupied by Deep stations. The North Assemblage not only moves southwards but starts to spread towards the east taking over a Main area to the east of Funk Island Deep; meanwhile the Coastal Assemblage is progressing slowly towards the east even in southern areas such as Funk Island Bank. Bottom temperatures in the Coastal and North groups are warmer than average whereas in the other two assemblages the mean surface temperatures are quite cold. Arctic cod increases sharply in the Coastal group this year. Some recovery of American plaice is observed in the North group this year, and this persists also into 1989. A substantial recovery of Atlantic cod in the North Assemblage was found this year though this species continued to decline in the Coastal and Main groups. Broadhead wolffish increases slightly in the Deep and North groups.

Autumn 1989

The Coastal group keeps invading Main areas to the east especially around St. Anthony Basin in this year. The same trend is found with the North stations which are even south of Funk Island Deep as well as the Main Assemblage taking over areas

spatially characteristic of the Deep group as in 1988 but now progressing towards the east. Mean surface temperatures in all the assemblages remain colder than the average values in the years of the first period. Blue hake reaches its lowest level of abundance in the Deep Assemblage over all years. In this year are also found the lowest abundance values for Greenland halibut in the Coastal and Deep Assemblages and for Broadhead wolffish in the Deep Assemblage. No Thorny skate was caught in the Coastal Assemblage and a significant increase of Atlantic cod in the Main group was found. American plaice had the lowest CPUE value in the Coastal group ever encountered in this study with only 2 kg/tow as a mean. Arctic cod abundance in 1989 was the highest for the Coastal group, showing some recovery from the previous three years in the North.

Autumn 1990

Very few stations classified with North group characteristics were found in the area north of Hawke Saddle which was normally occupied by that assemblage; stations within the mean North zone are mainly of Coastal composition showing only North characteristics in the area between Hamilton Bank and the continental slope normally occupied at that latitude by the Deep group. Some scattering of North stations is found towards the south in amongst the Main areas, with the latter invaded by the Coastal group mainly at Belle Island Bank and Funk Island Bank. Quite cold mean surface temperature for the Main group occurs this year. There is a sharp decline of Arctic cod in the Coastal and North groups. The lowest value of abundance found for Striped wolffish was found in the Main area. Spotted wolffish and American plaice decrease in the Main and North groups and Atlantic cod does the same in the Coastal Assemblage. Thorny skate recovers slightly in the Coastal group but decreases in the Main. Greenland halibut recovers in abundance somewhat in comparison to the preceding year in the Deep and Coastal Assemblages but decreases in the North and Main groups. Marlin spike and Blue hake increase in abundance slightly in the Deep Assemblage.

Autumn 1991

Stations with species composition and abundance characteristic of the Main Assemblage have practically disappeared from the western part of their mean distribution area, and are concentrated mainly to the east alongside the Deep Assemblage and in some cases taking it over. Three areas remain that display the original composition of the mean Main Assemblage's spatial distribution, those being Funk Island Deep, Hawke Saddle and the southern part of Funk Island Deep. The Coastal group has taken over Hamilton and Harrison Banks, formerly North Assemblage areas, with a few North stations remaining still to the east of Hamilton Bank and between the latter and the Deep group area and scattered on Belle Island Bank where they have taken over Main group areas. As a consequence of these changes, three different holes can be seen in the spatial distribution of the fish assemblages where the Coastal group has taken the spatial areas occupied by other groups in the first period of study. At Hamilton Bank it invades the North group and at the south of Hawke Saddle and to the east of Funk Island Deep on Funk Island Bank it takes over the Main Assemblage. Warmer than average values are found for bottom temperature in the Coastal, Main and North Assemblages.

Marlin spike and Witch flounder have continued to increase their abundance in the Deep group though the former's CPUE scale is very low. Greenland halibut decreases in all the assemblages showing its lowest ever value in the North Assemblage. Thorny skate shows the least abundance in the Main group in 1991, and Broadhead wolffish does the same in the Main and North Assemblages. Cod CPUE decreases to practically zero in the North group but maintains an average of 160 kg/tow in the Main Assemblage. American plaice decreases to very low levels of abundance in those assemblages where it is a characteristic species and the same happens with Deepwater redfish, Spotted wolffish, Arctic eelpout and Golden redfish. Roughhead grenadier increases to the maximum value in the Deep group since 1979, but at the same time displays its lowest values in the Main and North Assemblages. Roundnose grenadier recovers slightly from its low in 1987 to reach a value around the mean. Arctic cod

increases its abundance slightly in the Coastal and North group and the same happens to the Striped wolffish in the Main group.

CHAPTER 5. SPATIAL CHANGES OF FISH ASSEMBLAGES

5.1 Persistence and Fidelity

Four different groundfish assemblages that persisted over fourteen years were identified on the Northeast Newfoundland and Labrador shelf using a classification analysis based on biomass data. Deepwater redfish and Greenland halibut were the species found mainly in deeper waters while Atlantic cod, American plaice, Thorny skate and Witch flounder were found at intermediate and shallow depths. Some species had the limits of their distribution aligned with assemblage contours; thus, Atlantic cod, Witch flounder, American plaice and Thorny skate disappear as we move from the Main to the Deep Assemblage, there are no wolffishes in the Coastal Assemblage and there are no Deepwater redfish or Roughhead grenadier in the North Assemblage.

Though different authors have found that assemblages similar to those reported here were homogeneous throughout their study period, they had not studied them during a period of dramatic changes in species diversity and, especially, abundance. Fidelity to space, defined as the property of assemblages to keep within certain geographic boundaries, is evident only during the first nine years of the Northeast Newfoundland and Labrador time series data. Assemblage contours are located virtually in the same geographic positions in each of these years. The analyses for the last five years display higher variability in the spatial distribution of some of the assemblages. These begin somewhat earlier in the North in subarea 2J, where they are coincident with a reduction of some of the most important commercial species (Bishop et al., 1993). The Main Assemblage moves East and concentrates in small areas by the slope break, and the

Coastal Assemblage takes over most of the areas covered previously by the North and Main Assemblages. During this time it may be that a combination of anthropogenic and environmental factors have influenced the distributions of the groundfish species studied. Recent studies at population levels also show important spatial changes in species biomass in NAFO subarea 3L, the Grand Banks shelf where Gomes (1993) found persistent and homogeneous assemblages. His investigations ended in 1987; it is likely that he would have found a displacement of the assemblages similar to those encountered on the Northeast Newfoundland shelf if his analyses were repeated today. Assemblages that exhibit fidelity to space may be characteristic of non-disturbed ecosystems.

An alternative perspective on the changes in most of the spatial distributions of the assemblages would be to regard the groupings of fish as comprised of those remaining after overfishing the area. So far we have considered a dynamical perspective where species and populations are thought to move and thereby change local abundance; we may also take a static view and regard changes in abundance as reflections mostly of local depletions. If we think of the abundance of the commercial species composing the assemblages, the Coastal Assemblage is the least diverse with the smallest biomass followed by the Main and North which show an increase in both CPUE and diversity. The Deep Assemblage is the most diverse although Atlantic cod, which is the cornerstone of the fishery in the Northeast Newfoundland and Labrador shelf, is not present in any numbers. Thus, there is an increase in diversity and CPUE as we go towards the East and away from the shore. Since the concentrations of fish eventually ended up at the shelf-break, i.e. far to the east, there is a depletion of fish on the shelf which translates into an apparent advance of the less diverse and less abundant assemblages towards the East to take over the areas previously occupied by the more diverse assemblages. The above explanation does not apply so much to the Deep Assemblage because it occupies deeper areas and therefore contains more characteristically deep-sea species. The decrease of the commercial species and some non-commercial species in the assemblages can be due mainly to two anthropogenic factors: 1) an increase in the fishing efficiency

probably as a result of the better technology to detect fish, and a rise in the number of middle-sized offshore vessels; and 2) an increase in fish catchability since concentrations make them a more vulnerable target to the fishermen once they are detected; this density will increase the possibility of a higher catch in a shorter time and at relatively low effort thus depleting the stocks even more rapidly (Hutchings and Myers, 1994).

Another consequence of this static view of the results is that certain commercial species that are diminishing their size on the shelf as a whole (Morgan et al., 1993) are showing an increasing trend in their CPUE in some of the assemblages in spite of decreasing the spatial areal extent of the assemblage. This is again an effect of higher density in certain areas since abundance data reveal a decline in the fish size and length at age (Murphy and Bishop, 1993; Hutchings and Myers, 1994). This trend is not limited to commercial species, but is apparent in non-commercial species too; thus, older fish have been removed leaving only aggregations of younger fish mostly in restricted areas along the shelf-break, i.e. mainly to the East of the three major banks.

5.2 Possible Causes

Shifts in spatial distribution of the assemblages studied and sometimes a decline in the biomass of the component species could have been due to overfishing. Nonetheless, the fact that non-commercial species in the assemblages have declined too may indicate an overall broadscale trend (Savvatimsky, 1987). Environmental changes e.g. meteorological and oceanographic conditions (Baidalinov, 1989; Claireaux and Dutil, 1992; Narayanan et al., 1993), variability in the distribution and availability of prey (Bowering and Lilly, 1992; Lilly, 1987; Lilly et al., 1994; Lilly, 1994), increase in bycatch biomass (Albikovskaya, 1982), competition (Paz and Larrañeta, 1989), either alone or in any combination of these conditions could account for the observed situation. If that is the case, long-term perturbations in an ecosystem might be detected in the spatial variation of assemblages, which can behave as indicators at a greater scale than will single populations.

During the decade of the 70's, the 1970-72 period was one of generally declining surface temperature and salinities. The cooling trend persisted until 1975 but sea surface temperatures returned to near-normal levels by 1978 (Stein, 1982; Trites, 1982) and, at the same time, there are several reports of commercial fish declining in NAFO subareas 2J3KL. There has been a general cooling trend in the temperature of the water column on the Northeast Newfoundland and Labrador shelf starting in 1983 (Petrie et al., 1992). The last year of groundfish data analysis (1991) presented an extreme situation in both the biotic (great distortion of the mean spatial distribution of the assemblages, Chapter 3) and abiotic variables; annual air temperature anomaly pattern showed very cold conditions with negative anomalies of over 2°C and there was early ice formation and presence of many icebergs. This, together with strong northwesterly winds and cold air temperatures throughout the winter, generated an ice duration two months longer than normal at sites near the coast (Drinkwater et al., 1992; Sigaev, 1993). Narayanan et al. (1992) described bottom temperatures on the continental shelf as below normal in the 1983-1985 period, improving slightly in 1986 and 1987 and cooling again from 1988 to 1991; thus, 1991 was the final result of the cooler conditions that had been encountered in 1983 and that persisted into 1992 (Drinkwater, 1993). Narayanan et al. (1992) used the data from an oceanographic mooring program that was established on Hamilton Bank to monitor the Labrador Current. The temperature measured on the bank indicated below normal conditions from 1983 to 1986; the authors remark that they never encountered similar variability at an offshore location. Moored instrument measurements taken in the deep channels that separate the other two major banks in 2J3K, i.e. Belle Isle and Funk Island Banks, showed that the bottom temperature in these channels was well above zero throughout the year but was cooler on the banks.

Regarding the year-to-year variation in the spatial distribution of the assemblages, it can be appreciated that, beginning approximately in 1983, there is an intrusion of the Coastal Assemblage onto Hamilton Bank, an area occupied by the North Assemblage in the preceding years (1978-1982). This intrusion persisted with certain variations over

the following years, and from 1986 on there was an increasing occupation of all the major bank areas by the Coastal Assemblage. Thus, Belle Isle Bank and Funk Island Bank are almost taken over by the Coastal Assemblage in 1991 with a resulting decrease of the biomass of some of the very important commercial species (Bishop and Baird, 1993) and the disappearance of some non-commercial species such as the wolffishes. Whether this takeover is due to temperature variation is difficult to answer with the data obtained just from fall surveys (Anderson, 1993); temperature values measured at the time when the fish were caught are not necessarily representative of the mean value in the station sampled.

In the autumn, the cold intermediate layer (CIL) undergoes rapid warming and there are some inshore stations where the CIL reaches to the bottom; Smith et al. (1991) found interannual changes in the estimated abundance from surveys coincident, in a number of cases, with changes in the proportion of the bottom water composed by the CIL. I did not consider it appropriate to use data from Station 27, a station situated near St. John's where data has been recorded continuously for 50 years, in this case because the 213K shelf has a very rugged topography and there is a great influence from the offshore Labrador Current along the shelf edge which induces oscillations of the shelf water/slope water front there (Narayanan et al., 1992). The local variability that results from the topography and such oscillations (Helbig et al., 1992) would not be seen in any smoothed generalization based on Station 27 data.

Plots of the mean bottom temperatures of the stations within each assemblage every year (Fig. 5-1) suggest a stable average temperature value for the Deep and Main Assemblage, the two which show a higher mean CPUE. Since the Deep Assemblage is concentrated along the edge of the slope, it has very characteristic deepwater species and physical features. Values for the bottom temperature were fairly stable between 3 and 4°C for most of the fourteen years. The Main Assemblage is more controversial since it has grown smaller spatially since 1986 but somehow has shown a higher concentration of biomass, maintaining the CPUE but reducing the area covered. Average bottom

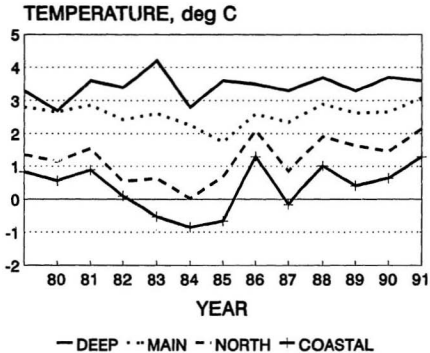


Figure 5-1. Mean bottom temperatures recorded at survey stations in each assemblage area by year.

temperature which fluctuates between 2 and 3°C declined in 1985 but recovered its mean value for the subsequent years; the recovery was due mainly to the fact that most of the stations belonging to this assemblage are situated towards the East from 1986 onwards and the eastern part of the shelf exhibits generally warmer temperatures. On the other hand, the North and Coastal Assemblages show lower temperatures and both seem to have gone through three different stages during the fourteen-year study period; as mentioned before, meteorological and oceanographical conditions have produced an increase of ice extent, icebergs and below normal temperatures which have affected

mostly the areas covered by the North and Coastal Assemblages. From 1978 until 1981, quite stable average bottom temperatures were measured but starting in 1981 and until 1984 there was a sharp decrease that reached 0°C in the North Assemblage and -1°C in the Coastal one; between 1984 and 1991 there seems to have been a general increasing temperature trend to reach values similar to those found in the first four years analyzed (except for 1987 and 1989 which were cooler).

If higher CPUE values are found in areas with quite stable temperatures, it could be possible that groundfish avoid areas with higher variation of bottom temperature on the one hand, and look for warmer ones in the other hand. Jobling (1988) in a study concerning growth of cod under farmed conditions mentions ". . . within the thermal tolerance zone, fish, if given a choice, will elect to spend most time within water of a certain temperature and these preferred temperatures are dependent upon acclimation temperature . . .". He also found that for cod the preferred temperature range coincides with the range of temperature within which most of their physiological processes are maximised. Since cod are the main component species of some of the assemblages (50% in the North Assemblage and 35% in the Main), the assemblage shifts may simply reflect cod behaviour which should, by Jobling's (1988) argument, show a tendency to shift to better conditions when there are sudden fluctuations in the temperature regime.

Anthropogenic factors may be affecting the groundfish distribution on the shelf at different life stages of the fish (Allen and McGlade, 1986; Anderson and Dalley, 1993). Middle-sized trawlers have increased the number of hours of trawling, especially from 1986 on, by about 20,000 hours in 2J3KL and the size of the cod fish being taken has decreased enormously; Hutchings and Myers (1994) found that the percentage of older components of the cod fishery decreased from 1962 to 1993, with the individuals 9 years old comprising only 1% of the total catch in 1993 in comparison to 2.5% in 1962. Several books and papers (Cushing and Harden Jones, 1968; Clark, 1974; Pitcher, 1993) report fish grouping behaviour for different reasons (e.g. spawning, food or protection), but this has been found mainly in pelagic fish; groundfish grouping has only

been reported for spawning cod and post-spawning schools of cod migrating inshore on the 2J3KL shelf during Spring/Summer (Rose, 1993). If overexploitation is decimating the groundfish populations on the Northeast Newfoundland and Labrador shelf, higher density grouping might be a reaction to ensure survival when there is a risk of intense predation. Fish started showing that tendency to form aggregations in 1986 on certain areas of the shelf and ended up in the last year of study being concentrated in groups along the shelf break. Since fishing intensified tremendously in the mid-80's, this behaviour may be an alternative state of self-regulation when the population is threatened; that is, a compensatory capacity to overcome exploitation. The characteristically high levels of recruitment variability in marine populations can easily obscure any evidence of underlying regulatory processes (Fogarty et al., 1991); thus, no evidence of such actions has been reported for groundfish so far since the strategy of most groundfish migrating offshore in the fall remains unknown.

Some of the less abundant species within the assemblages showed a decline earlier than the dominant commercial species. The latter are long-lived species that are dominant on the shelf and have for centuries survived the extreme conditions that appear stochastically as a result of natural environmental variability; therefore, they should be well adapted to adverse circumstances and their populations should normally exhibit naturally a certain stability. Only if the unfavourable conditions are very extreme and persistent over time will they be unable to recover and will decline. A few years will be needed to perceive the decline in the species but by then it may be too late to stop fishing and let the species recover (Walters and Holling, 1990). Rare but always present species are more likely to react earlier to changes, and will decrease sooner due to their low biomass and the fact that they probably occupy a somewhat narrower niche in the ecosystem; thus, they could act as early indicators of anomalies occurring on the shelf that the commercial species would not show until some later time. An example can be found with wolffish whose decrease in abundance started in 1982, well before the cod decline. We can also expect that these species will show a recovery ahead of the commercial ones

since it will take them less time to reach their mean biomass levels maintaining stability at lower abundance.

5.3 Final Comments and Future Work

Most of the results concerning assemblages found on the Northeast Newfoundland and Labrador shelf are driven by a cornerstone species, Atlantic cod, which is the main commercial target species in the fisheries. Since 1986, shifts in cod distribution have produced spatial variability in the distribution of three of the four assemblages. At the same time, big decreases in biomass have affected the other commercial species thereby increasing the overall apparent effect. Bottom temperature changes do not seem to have been extreme enough to affect older individuals, although sudden variations may have affected spawning and therefore number of recruits. At the same time, the removal of the older individuals has decreased the number of potential spawners (Hutchings and Myers, 1994).

Some environmental variables other than temperature have been tested to account for the declining biomass on the Northeast Newfoundland and Labrador shelf; summer salinity was found to be strongly correlated with cod recruitment, although the mechanism remains unknown (Myers et al., 1992); de Young and Rose (1993) suggested it was necessary ". . . to reassess the interactions between stock spatial dynamics and distributions, recruitment, abundance and environmental fluctuations as an alternative model of recent stock fluctuations . . .". Myers et al. (1993) explored the relation of cod spawning time to physical and biological cycles and found that spawning time decreased as latitude increased. Though many hypotheses concerning possible changes of the environment and its possible influence on groundfish distribution are being tested, none of them have given conclusive results to account for the dramatic changes in fish abundance and distribution on the shelf. Changing of weather as a whole should be taken into account as Aebischer et al. (1990) found parallel long-term trends across for marine trophic levels and weather during a 30 year-period.

The assemblage scale approach has proven useful to find biologically tractable areas that could be amenable to management at a scale below that of the whole shelf; species showing certain variations at a bigger scale may behave differently at a smaller scale where they display trends that a mean for the shelf or for subareas on the shelf would not show. This multispecies approach provides a spatial distribution vision that allows the mapping of the shelf and the identification of "hot spots" for species variation. The mean distributions of the groundfish assemblages are aligned with the bottom topography and reveal certain environmental gradients; further studies at the assemblage scale may show vital zones for fish species population dynamics such as nursery or spawning areas that should be managed cautiously and on a relatively fine scale.

Having detected spatial variation in the assemblages, the next step will be to attempt a higher resolution defining fixed areas on the shelf where there has been a shift noticed at the assemblage level. That will allow us to observe possible temporal variations in the biomass of species present and to make finer-scaled comparisons both North-South and East-West. Work of this sort could continue based on the data developed in this thesis. Both the assemblage approach and the area approach would provide a great deal of information on spatial changes in biomass and in temporal assemblage shifts that could be used to map the spatial density patterns of the main commercial and non-commercial species for proper management and stock rebuilding programs (Walters, 1994).

BIBLIOGRAPHY

- Aebischer N.J., J.C. Coulson, and J.M. Colebrook. "Parallel long-term trends across four marine trophic levels and weather." *Nature* 347 (25 October 1990): 753-755.
- Akenhead, S.A. and E.M. LeGrow. "The Vertebrate Code of the Northwest Atlantic Fisheries Centre." *Canadian Data Rept. Fish. Aquat. Sci.* no. 309 (1981): 1-58.
- Albikovskaya, L.K. "Distribution and Abundance of Atlantic Wolffish, Spotted Wolffish and Northern Wolffish in the Newfoundland Area." *NAFO Science Council Studies* 3 (1982): 29-32.
- Allen, P.M., and J.M. McGlade. "Dynamics of discovery and exploitation: The case of the Scotian Shelf groundfish fisheries." *Can. J. Fish. Aquat. Sci.* 43 (1986): 1187-1200.
- Anderson, J.T. "Distributions of Juvenile Cod in NAFO Divisions 2J3KL During Fall, 1981-92, in Relation to Bathymetry and Bottom Temperatures." *NAFO SCR Doc.* 93/68 Serial No. N2252 (1993): 1-18.
- Anderson, J.T. and E. Dalley. "Inshore/Offshore Distributions and Abundances of Pelagic O-Group Cod in NAFO Divisions 3K and 3L in Fall of 1991 and 1992." *NAFO SCR Doc.* 93/32 Serial No. N2212 (1993): 1-18.
- Atkinson, D.B. "Some Observations on the Biomass and Abundance of Fish Captured During Stratified Random Bottom Trawl Surveys in NAFO Divisions 2J3KL, Fall 1981-1991." *NAFO SCR Doc.* 93/29 Serial No. N2209 (1993): 1-18. [see also: *NAFO Science Council Studies* 21 (1994): 43-66.
- Baidalinov, A.P. "On the influence of long-term changes of environmental factors on the state of some fish populations stocks in the Northwest Atlantic." *NAFO SCR Doc.* 89/84 (1989). serial No. N1668.
- Bergstad, O.A. "Ecology of the fishes of the Norwegian Deep: Distribution and species assemblages." *Netherlands Journal of Sea Research* 25(1/2) (1990): 237-266.

- Bishop, C.A., and J.W. Baird. "Spatial and Temporal Variability in Condition Factors of 2J3KL Cod." *NAFO SCR Doc. 93/56* Serial NO. N2239 (1993): 1-15.
- Bishop, C.A., E.F. Murphy, M.B. Davis, J.W. Baird, and G.A. Rose. "An Assessment of the Cod Stock in NAFO Division 2J+3KL." *NAFO SCR Doc. 93/86* Serial No. N2271 (1993): 1-51.
- Boesch, D. "Application of numerical classification in ecological investigations of water pollution." *U.S. Environ. Protect. Agency Ecol. Res. Ser. EPA-600/3-77-033* (1977): 115 pp. Washington, DC.
- Bowering, W.R., and G.R. Lilly. "Greenland Halibut (*Reinhardtius hippoglossoides*) off Southern Labrador and Northeastern Newfoundland (Northwest Atlantic) Feed Primarily on Capelin (*Mallotus villosus*)." *Netherlands Journal of Sea Research* 29 (1992): 211-222.
- Claireaux, G., and J-D. Dutil. "Physiological Response of the Atlantic Cod (*Gadus morhua*) to Hypoxia at Various Environmental Salinities." *Journal of Experimental Biology* 163 (1992): 97-118.
- Clark, C. "Possible effects of schooling on the dynamics of exploited fish populations." *J. Cons. Perm. Int. Explor. Mer* 36 (1974): 7-14.
- Cochran, W.G. *Sampling techniques*, 428. New York: John Wiley and Sons, 1977.
- Cochran, M.E., and S. Ellner. "Simple Methods for Calculating Age-Based Life History Parameters for Stage-Structured Populations." *Ecological Monographs* 62 (1992): 345-364.
- Colvocoresses, J.A., and J.A. Musick. "Species associations and community composition on Middle Atlantic Bight continental shelf demersal fishes." *Fishery Bulletin* 82, no. 2 (1984): 295-313.
- Cushing D.H., and F.R. Harden Jones. "Why do fish school?." *Nature* 218 (1968): 918-20.
- Dalley, E.L., and J.T. Anderson. "Distribution and abundance of Demersal Juvenile cod from inshore to offshore locations on the Northern Grand Bank and NE Newfoundland shelf in December, 1992." *NAFO SCR Doc. 93/35* Serial No. N2215 (1993): 9 p.

- deYoung, B., and G.A. Rose. "On Recruitment and Distribution of Newfoundland Cod (*Gadus morhua*).¹" *Journal of Fisheries and Aquatic Sciences* (In press) (1993).
- Dickie, L.M., S.R. Kerr, and P. Schwinghamer. "An Ecological Approach to Fisheries Assessment." *Canadian Journal of Fisheries and Aquatic Sciences* 44 (1987): 69-74.
- Doubleday, W.G., and D. Rivard. "Workshop Report." Proceedings of a workshop on Bottom Trawl surveys. *Canadian Special Publication of Fisheries and Aquatic Sciences* 58 (1981): 13-258, edited by W.G. and D. Rivard Doubleday. Ottawa, Canada: DFO.
- Drinkwater, K.F. "Overview of Environmental Conditions in the Northwest Atlantic in 1992." *NAFO SCR Doc. 93/5* Serial No. N2231 (1993): 1-33.
- Drinkwater, K.F., B. Petrie, and S. Narayanan. "Overview of environmental conditions in the northwest Atlantic in 1991." *NAFO Sci. Coun. Studies* 20 (1992): 19-46.
- Fogarty, M.J., M.P. Sissenwine, and E.B. Cohen. "Recruitment variability and the dynamics of exploited marine populations." *Tree* 6, no. No. 8 (August 1991): 241-245.
- Frechet, A. "A Declining Cod Stock in the Gulf of St. Lawrence: How Can We Learn From the Past?." *NAFO Science Council Studies* 16 (1991): 95-102.
- Gabriel, W.L., and A.V. Tyler. "Preliminary Analysis of Pacific Coast Demersal Fish Assemblages." *Marine Fisheries Review*, March-April 1980, 83-88.
- Gauch, H.G., and R.H. Whittaker. "Hierarchical classification of community data." *J. Ecol.* 69 (1981): 537-557.
- Gauch, H.G. Jr. *Multivariate Analysis in Community Ecology*. Cambridge: Cambridge University Press, 1982.
- Gomes, M.C. "Analise Factorial em Ecologia. Aplicacao ao estudo da Fauna Demersal da Costa Portuguesa.," 149 pp. Fac. Sci. of Lisbon Univ., Lisbon, Portugal: M.Sc.Thesis., 1987.
- Gomes, M. do C. *Predictions Under Uncertainty: fish assemblages and food webs on the Grand Banks of Newfoundland*. [Ph.D. thesis, Memorial University, 1991]. 205 pp., St. John's, Newfoundland: ISER Books, 1993.

- Gomes, M.C., R.L. Haedrich, and J.C. Rice. "Biogeography of Groundfish Assemblages on the Grand Bank." *Journal of Northwest Atlantic Fishery Sciences* 14 (1992): 13-27.
- Helbig J., Mertz G., and P. Pepin. "Environmental influences on the recruitment of Newfoundland/Labrador Cod." *Fisheries Oceanography* 1, no. 1 (1992): 39-56.
- Hilborn R., and C.J. Walters. *Quantitative Fisheries Stock Assessment*. New York: Chapman & Hall, 1992.
- Hill, M.O.. "Reciprocal averaging: an eigenvector method of ordination." *J. Ecol.* 61 (1973): 237-249.
- Hill, M.O. "Use of simple discriminant functions to classify quantitative phytosociological data." In *First International Symposium on Data Analysis and Informatics, Versailles 7-9 Sept. 1977*, edited by E. Diday, L. Lebart, J.P. Pages and R. Tamassone, 181-199 (1977).
- Hill, M.O. "TWINSPAN-A FORTRAN Program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes." In *Ecology and Systematics*. Ithaca, NY, USA: Cornell Univ., 1979.
- Hill, M.O., R. Bunce, and M. Shaw. "Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland." *J. Ecol.* 63 (1975): 597-613.
- Hutchings, J.A., and R.A. Myers. "What can be learned from the collapse of a renewable resource?, Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador." In *Canadian J. Fish. Aquat. Sci.* 51, (in press) (1994).
- Jobling, M. "A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions." *Aquaculture* 70 (1988): 1-19.
- Lambert, J., S. Meacock, J. Barrs, and P. Smartt. "AXOR and MONIT: two new polythetic divisive strategies for hierarchical classification." *Taxon* 22 (1973): 173-176.
- Lazier, J.R.N. "Seasonal variability of temperature and salinity in the Labrador Current." *J. Mar. Res.* 40 (1982): 341-356.

- Lilly, G.R. "Predation by Atlantic cod on capelin on the Southern Labrador and Northeast Newfoundland shelves during a period of changing spatial distributions." *ICES mar. Sci. Symp.* 198 (in press) (1994): 23p.
- , "Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review." *Can. Tech. Rep. Fish. Aquat. Sci.* 1567 (1987): vii + 37p.
- Lilly, G.R., H. Hop, D.E. Stansbury, and C.A. Bishop. "Distribution and abundance of polar cod (*Boreogadus saida*) off southern Labrador and eastern Newfoundland." *ICES C.M.* 1994/O:6 (1994).
- Ludwig, D., R. Hilborn, and C. Walters. "Uncertainty, Resource Exploitation and Conservation: Lessons from History." *Science* 260 (April 1993): 17,36.
- Mahon, R., and R.W. Smith. "Demersal Fish Assemblages on the Scotian Shelf, Northwest Atlantic: Spatial Distribution and Persistence." *Canadian Journal of Fisheries and Aquatic Sciences* 46 (1989): 134-152.
- Messiah, S.N. "Changes in the Gulf of St. Lawrence Herring Populations in the Past Three Decades." *NAFO SCR Doc.* 89/74 Serial No. N1655 (1989): 1-47.
- Morgan, M. J., C.A. Bishop, and J.W. Baird. "Temporal and Spatial Variations in Age and Length at Maturity in 2J3KL Cod." *NAFO SCR Doc.* 93/57 Serial No. N2240 (1993): 1-8.
- Mueller-Dombois, D., and H. Ellenberg. *Aims and Methods of Vegetation Ecology*. Wiley, New York, 1974.
- Murphy, E.A., and C.A. Bishop. "Cod in Divisions 2J+3KL - Estimates of Biomass and Age Composition for the Portion of the Stock in the NAFO Regulatory Area." *NAFO SCR Doc.* 93/47 Serial No. N2228 (1993): 1-8.
- Myers, R.A., G. Mertz, and C.A. Bishop. "Cod spawning in relation to physical and biological cycles of the northern northwest Atlantic." *Fisheries Oceanography* 2 (1993): 154-165.
- Myers, R.A., K. Drinkwater, and S. Brown. "The Influence of Salinity on 2J3KL Cod Recruitment." *NAFO SCR Doc.* 92/74 Serial No. N2129 (1992): 1-12.

- Narayanan, S., J.W. Bair, C.A. Bishop, and G.R. Lilly. "Climate Effects on Cod Distribution Deduced from Trawl Surveys." *NAFO SCR Doc. 93/33* Serial No. N2213 (1993): 1-8.
- Narayanan, S., S. Prinsenber, and E.B. Colbourne. "Overview of environmental conditions in 2J3KL NAFO subareas in 1991." *NAFO SCR Doc. 92/6* Serial No. N2039 (1992): 1-30.
- Overholtz, W., J., and A.V. Tyler. "Long-Term Responses of the Demersal Fish Assemblages of Georges Bank." *Fishery Bulletin* 83 (1985): 507-520.
- Paz, J., and M.G. Larrañeta. "Cod in Div. 3NO: Year Class Variations and the Abundance of Other Commercial Fish." *NAFO SCR Doc. 89/72* Serial No. N1653 (1989): 1-9.
- Petrie, B., J.W. Loder, J. Lazier, and S. Akenhead. "Temperature and salinity variability on the Eastern Newfoundland shelf- The residual field." *Atmosphere-Ocean* 30, no. 1 (1992): 120-139.
- Petrie, B., and C. Anderson. "Circulation on the Newfoundland Continental Shelf." *Atmosphere-Ocean* 21 (1983): 207-226.
- Pielou, E.C. *Population and Community Ecology: Principles and Methods*. New York: Gordon and Breach, Science Publishers, 1974.
- , *The Interpretation of Ecological Data - A Primer on Classification and Ordination*. 263 pp. New York: John Wiley and Sons, 1984.
- Pimm, S.L. "Properties of food webs." *Ecology* 61 (1980): 219-225.
- Pitcher, T.J. "The Behaviour of Teleost Fishes." 2nd, 713. London: Chapman & Hall, 1993.
- , "The role of schooling in fish capture." *ICES CM* 1979/ B:5 (1979): 1-12.
- Pitt, T.K., R. Wells, and W.D. McKone. "A Critique of Research Vessel Otter Trawl Surveys by the St. John's Research and Resource Services." *Proceedings of a Workshop on Bottom Trawl Surveys, Canadian Special Publication of Fisheries and Aquatic Sciences* 58 (1981): 258, edited by W.G and D. Rivard Doubleday. Ottawa, Canada: DFO.

- Rogers, J.B., and J.B. Pikitch. "Numerical Definition of Groundfish Assemblages Caught Off the Coasts of Oregon and Washington Using Commercial Fishing Strategies ." *Canadian Journal of Fisheries and Aquatic Sciences* 49 (1992): 2648-2656.
- Rose, G.A. "Cod spawning on a migration highway in the north-west Atlantic." *Nature* 366 (2 December 1993): 458-461.
- Rosenberg, A.A., M.P. Fogarty, M.P. Sissenwine, J.R. Beddington, and J.G. Sheppard. "Achieving Sustainable Use of Renewable Resources." *Science* 262 (5/November 1993): 828-829.
- Savvatimsky, P.I. "Changes in Species Composition of Trawl Catches by Depth on the Continental Slope from Baffin Island to Northeastern Newfoundland, 1970-85." *NAFO Science Council Studies* 11 (1987): 43-52.
- Shelton P.A., G.R. Lilly and V. Christensen (rapporteurs). Ecopath Workshop entitled "A bulk biomass model for the Newfoundland-Labrador Shelf". DFO, St. John's (Newfoundland, Canada), 14-22 October 1993.
- Sigaev, I.K. "Oceanographic Conditions in Some Areas of the Northwest Atlantic in 1992." *NAFO SCR Doc. 93/1* Serial No. N2176 (1993): 1-5.
- Smith, S.J., R.I. Perry, and L.P. Fanning. "Relationships between water mass characteristics and estimates of fish population abundance from trawl surveys." *Environmental Monitoring and Assessment* (1991).
- Smith, S.J. "Use of Statistical Models for the Estimation of Abundance from Groundfish Trawl Survey Data." *Canadian Journal of Fisheries and Aquatic Science* 47 (1990): 894-903.
- Stein, M. "Autumn temperature anomalies of the Labrador current, 1969-80." *NAFO Sci. Coun. Studies* 5 (1982): 79-80.
- Trites, R.W. "Overview of Oceanographic Conditions in NAFO Subareas 2, 3 and 4 During the 1970-79 Decade." *NAFO Science Council Studies* 5 (1982): 51-78.
- Tyler, A.V., W.L. Gabriel, and W.J. Overholtz. "Adaptive Management Based on Structure of Fish Assemblages of Northern Continental Shelves." *Canadian Special Publication of Fisheries and Aquatic Sciences* 59 (1982): 149-156.

- Underwood, A.J. "What Is a Community?," Patterns and Processes in the History of Life, Dahlem Konferenzen 1986, edited by D.M. Raup and D. Jablonski. Heidelberg: Springer-Verlag Berlin, 1986.
- Walters, C.J. "Cod Off Eastern Canada: Lessons for Stock Assessment and Stock Rebuilding Programs." (*pers. comm.*) (1994). Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, B.C.,
- Walters, C.J., and C.S. Holling. "Large-Scale Management Experiments And Learning By Doing ." *Ecology* 71, No. 6 (1990): 2060-2068.
- Westhoff, V., and E. van der Maarel. "The Braun-Blanquet approach." In *Ordination and Classification of Communities*, edited by R.H. Whitehead, 617-726. Junk, The Hague, 1973.
- Wishart, D. *CLUSTAN User Manual*. Third edition. Edinburgh, Scotland: Program Library Unit, University of Edinburgh, 1978.

APPENDIX 1

I include in this appendix the values for total Autumn species biomass and abundance per assemblage (Coastal, Deep, Main and North) and year (1978-1991) that were used in the multispecies analysis. The species are classified by number (taxonomic order) according to the Department of Fisheries and Oceans code (Akenhead and LeGrow, 1981). Two lists with the code number and the common and scientific name of each species are supplied at the beginning; the first displays the species used in the analysis whereas the second shows species that appeared in the trawls but were not used for several reasons stated in the methodology. Abundance is reported in numbers and biomass in kilograms.

I include in this appendix the values for total Autumn species biomass and abundance per assemblage (Coastal, Deep, Main and North) and year (1978-1991) for all species that were taken in the surveys. The species are classified by number (taxonomic order) according to the Department of Fisheries and Oceans code (Akenhead and LeGrow, 1981); abundance is reported in numbers and biomass in kilograms. A list with the code number and the common name is supplied at the beginning for those species that were used in the multispecies analyses.

LIST OF SPECIES USED IN THE ANALYSIS ORDERED BY CODE (DFO)

Common name	Code	Scientific name
Dogfish, Black	27	<i>Centroscyllium fabricii</i>
Skate, Thorny	90	<i>Raja radiata</i>
Skate, Smooth	91	<i>Raja senta</i>
Skate, Spinytail	102	<i>Bathyraja spinicauda</i>
Capelin	187	<i>Mallotus villosus</i>
Eel, Longnose	373	<i>Synaphobranchus kaupii</i>
Tapirfish, Large Scale	386	<i>Notacanthus chemnitzii</i>
Hake, Blue	432	<i>Antimora rostrata</i>
Cod, Atlantic	438	<i>Gadus morhua</i>
Cod, Greenland	439	<i>Gadus ogac</i>
Cod, Arctic	451	<i>Boreogadus saida</i>
Grenadier, Roughhead	474	<i>Macrourus berglax</i>
Marlin Spike, Common	478	<i>Nezumia bairdii</i>
Grenadier, Roundnose	481	<i>Coryphaenoides rupestris</i>
Grenadier, Roughnose	483	<i>Trachyrhynchus murrayi</i>
Wolffish, Broadhead	699	<i>Anarhichas denticularis</i>
Wolffish, Striped	700	<i>Anarhichas minor</i>
Wolffish, Spotted	701	<i>Anarhichas lupus</i>
Eelpout, Esmarck's	727	<i>Lycodes esmarki</i>
Eelpout, Arctic	729	<i>Lycodes reticulatus</i>
Eelpout, Vahl's	730	<i>Lycodes vahlii</i>
Redfish, Golden	793	<i>Sebastes marinus</i>
Redfish, Deep Water	794	<i>Sebastes mentella</i>
Sea raven	809	<i>Hemirhamphus americanus</i>
Sculpin, Arctic Hookear	810	<i>Arctidiellus uncinatus</i>
Sculpin, Moustache	814	<i>Triglops murrayi</i>
Sculpin, Shorthorn	819	<i>Myoxocephalus scorpius</i>
Sculpin, Arctic Deepsea	829	<i>Cottunculus microps</i>
Alligatorfish, Northern	836	<i>Agonus decagonus</i>
Lumpfish, Spiny	844	<i>Eumicrotremus spinosus</i>
Lumpfish, Common	849	<i>Cyclopterus lumpus</i>
Plaice, American	889	<i>Hippoglossoides platessoides</i>
Flounder, Witch	890	<i>Glyptocephalus cynoglossus</i>
Halibut, Greenland	892	<i>Reinhardtius hippoglossoides</i>
Halibut, Atlantic	893	<i>Hippoglossus hippoglossus</i>

LIST OF SPECIES APPEARING IN THE DATA BUT NOT USED IN THE ANALYSIS ORDERED BY CODE (DFO).

Common name	Code	Scientific name
Deepwater Skate	94	<i>Raja fyllae</i>
Atlantic Herring	150	<i>Clupea harengus</i>
Black Herring	167	<i>Bathyractes sp.</i>
Blacksmelt	200	<i>Bathylagus sp.</i>
Goitre Blacksmelt	202	<i>Bathylagus euryops</i>
Viperfish	227	<i>Chauliodus sloani</i>
Boa Dragonfish	230	<i>Stomias boa ferox</i>
Lanternfish	272	Myctophidae
Scopelosaurus	300	Scopelosauridae
Barracudinas	316	Paralepididae
Barracudina	317	<i>Paralepis sp.</i>
Short Barracudina	318	<i>Paralepis brevis</i>
Scaled Lancetfish	320	<i>Notolepis rissoi krøyeri</i>
Shortnosed Lancetfish	324	<i>Alepisaurus brevirostris</i>
Snubnose Eels	358	Simenchelyidae
Snipe Eels	367	Nemichthyidae
Atlantic Snipe Eel	368	<i>Nemichthys scolopaceus</i>
Shortnose Snipe Eel	369	<i>Serrivomer beani</i>
Cutthroat Eels	372	Synaphobranchidae
Spiny Eels	384	Notocanthiformes
Spiny Eels	385	Notocanthidae
Shortspine Tapirfish	387	<i>Macdonaldia rostrata</i>
Longfin Hake	444	<i>Urophycis chesteri</i>
Threebeard Rockling	453	<i>Gaidropsarus sp.</i>
Threebeard Rockling	454	<i>Gaidropsarus ensis</i>
Cusk	458	<i>Brosme brosme</i>
Fourbeard Rockling	461	<i>Enchelyopus cimbrius</i>
Longnose Grenadier	482	<i>Coelorhynchus carminatus</i>
Bigeyes	609	Priacanthidae
Pricklebacks	709	Stichaeidae
Blenny	714	<i>Lumpenus sp.</i>
Snake Blenny	716	<i>Lumpenus lampretaeformis</i>

LIST OF SPECIES APPEARING IN THE DATA BUT NOT USED IN THE ANALYSIS ORDERED BY CODE (DFO) (cont.).

Common name	Code	Scientific name
Wrymouth	721	<i>Cryptacanthodes macularus</i>
Eelpout	726	<i>Lycodes sp.</i>
Laval's Eelpout	728	<i>Lycodes lavalei</i>
Eelpout	738	<i>Lycodes mucosus</i>
Wolf Eel	747	<i>Lycenchelys sp.</i>
Atlantic Hookear Sculpin	811	<i>Artediellus atlanticus</i>
Mailed Sculpin	813	<i>Triglops sp.</i>
Longhorn Sculpin	820	<i>Myoxocephalus octodecemspinosus</i>
Arctic Sculpin	822	<i>Myoxocephalus scorpioides</i>
Arctic Staghorn Sculpin	823	<i>Gymnocanthus tricusplis</i>
Deepsea Sculpin	827	<i>Cottunculus sp.</i>
Pallid Deepsea Sculpin	828	<i>Cottunculus thomsoni</i>
Common Alligatorfish	838	<i>Aspidophoroides monopterygius</i>
Lumpfish	843	<i>Eumicrotremus sp.</i>
Seasnails	853	Liparidae
Seasnail	857	<i>Liparis sp.</i>
Gelatinous Seasnail	859	<i>Liparis fabricii</i>
Striped Seasnail	860	<i>Liparis liparis</i>
Greenland Kelp Seasnail	861	<i>Liparis tunicatus</i>
Seasnail	863	<i>Careproctus sp.</i>
Seasnail	865	<i>Careproctus reinhardi</i>
Sea Tadpole	866	<i>Careproctus ranulus</i>
Sea Devils	980	Ceratiidae

COAST 1978			COAST 1979		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	51	27.04	90	3	3.63
438	218	357.29	438	29	53.56
451	50	2.10	439	2	0.45
701	3	23.61	451	5	0.14
729	23	18.42	699	6	63.55
730	62	12.48	701	1	12.71
794	7	0.32	819	1	0.45
829	2	0.23	836	1	0.05
836	43	1.37	843	1	0.14
844	3	0.10	849	2	4.54
849	2	3.41	889	226	60.83
889	1474	406.78	892	20	9.31
890	8	3.28			
892	2065	1111.84			

COAST 1980			COAST 1981		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	32	34.65	90	73	77.50
187	11420	360.50	187	2092	66.86
438	233	767.75	324	8	0.81
439	3	2.00	438	510	923.50
451	1602	22.55	451	285	8.16
474	8	9.00	699	2	18.00
699	14	141.70	700	20	26.30
701	13	68.50	701	6	43.50
726	33	27.40	729	31	30.70
727	8	1.00	730	17	5.05
730	5	1.55	794	6	0.61
794	9	1.50	820	5	3.00
827	6	0.50	836	7	0.51
849	9	21.00	849	6	11.80
889	522	197.80	889	1704	938.00
892	2000	1325.75	890	11	19.50
			892	1306	583.75

COAST 1982			COAST 1983		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	168	140.10	90	30	22.10
102	2	4.70	187	56	1.12
187	723	20.98	438	869	965.05
316	5	0.50	439	6	6.80
317	1	0.20	451	687	22.89
438	1354	2160.70	699	2	21.50
439	6	6.50	701	2	12.50
451	990	20.36	729	36	22.40
474	20	28.00	730	30	3.77
699	39	387.00	794	1	2.00
700	12	15.40	819	1	1.20
701	26	153.00	836	3	0.14
729	62	55.60	844	9	0.22
730	22	5.35	849	2	4.80
794	59	7.36	861	2	0.35
809	1	3.50	863	3	0.70
819	6	8.60	865	2	0.08
827	12	3.30	889	1993	1022.30
829	5	1.40	890	26	36.60
836	6	0.32	892	667	278.00
843	18	1.22	893	1	1.75
849	7	25.90			
859	3	0.60			
889	3894	1690.00			
890	20	25.70			
892	3055	1728.50			
893	1	3.50			

COAST 1984			COAST 1985		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	56	71.25	90	90	4727.00
187	192	5.23	187	169	425.00
320	4	0.35	438	3741	401960.00
438	3722	4926.60	439	13	1235.00
439	7	5.15	451	7613	18743.00
451	1584	55.92	474	3	165.00
699	5	52.00	699	2	1400.00
700	19	28.80	700	13	1350.00
701	11	79.00	701	1	550.00
729	132	87.25	729	76	5370.00
730	14	3.00	730	15	210.00
794	5	0.80	794	13	166.00
813	5	0.16	810	27	53.00

819	4	3.80	836	39	135.00
836	12	1.26	843	12	135.00
844	62	4.55	844	57	298.00
849	4	6.60	849	23	5975.00
860	5	0.50	853	14	232.00
863	22	1.87	857	13	167.00
889	2544	1158.30	859	21	305.00
892	564	330.05	889	2894	120435.00
			890	5	670.00
			892	1416	56796.00

COAST 1986			COAST 1987		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	69	24.60	90	57	35.35
102	1	12.00	187	623	11.77
187	1232	32.54	316	6	0.10
438	1941	2706.60	438	2261	3218.20
451	1904	51.86	439	7	4.10
700	5	5.10	451	1367	48.91
701	3	18.50	699	1	13.00
729	36	23.85	701	4	33.00
730	39	7.70	727	5	0.40
794	13	1.25	729	71	45.35
809	1	2.70	730	40	6.77
810	7	0.11	794	5	0.46
819	4	2.90	809	2	2.80
836	16	0.62	810	6	0.11
843	24	1.75	813	7	0.13
849	85	219.60	836	29	1.04
853	7	1.70	838	1	0.01
889	873	378.35	843	8	0.18
890	8	7.05	844	9	0.25
892	1391	714.73	849	14	38.80
			861	8	0.71
			863	24	2.25
			889	1533	652.15
			890	23	13.20
			892	2855	1236.55

COAST 1988			COAST 1989		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	130	89.23	90	197	78.74
102	2	6.30	91	4	1.64
187	2477	40.92	102	1	5.25
438	1473	2335.68	187	1674	50.97
451	8722	160.89	438	1210	998.27
474	1	2.60	439	9	6.16
699	2	32.50	451	5962	237.53
701	1	3.00	699	5	51.00
729	105	78.95	700	14	12.69
730	50	6.51	701	4	9.20
810	11	0.13	727	20	2.04
813	8	0.15	729	205	106.06
819	11	7.80	730	94	11.08
827	11	1.50	794	24	3.26
836	30	0.82	809	2	2.39
838	1	0.01	810	27	0.61
843	20	0.84	813	54	0.72
844	31	1.16	819	20	8.65
849	179	390.25	827	12	1.34
853	16	2.41	836	51	1.32
859	1	0.02	838	8	0.07
863	38	1.83	843	77	4.33
889	798	336.23	844	144	5.67
890	25	23.80	849	73	168.36
892	1981	718.24	853	40	5.44
			861	22	3.29
			889	610	204.91
			890	21	7.90
			892	2335	850.26
			893	1	3.60

COAST 1990			COAST 1991		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	215	86.72	90	423	165.08
91	2	1.75	91	8	2.80
102	7	61.40	102	2	3.24
187	528	15.05	187	5111	103.69
438	1089	598.80	316	25	0.49
451	1659	56.24	320	30	1.08
474	5	3.06	438	4292	3140.00
699	3	35	451	5403	90.60
700	5	1.81	474	15	6.60
701	2	9.00	700	29	24.06
729	82	44.42	701	6	7.57

730	78	8.48	729	108	45.05
794	37	9.57	730	80	8.56
810	15	0.16	794	76	15.27
813	11	0.18	810	29	0.64
819	19	10.94	813	27	0.49
829	14	2.31	819	13	8.79
836	76	2.71	829	46	8.24
843	92	5.54	836	108	3.29
844	20	1.18	838	24	0.82
849	45	81.90	843	26	2.25
853	31	1.64	849	33	58.18
861	17	1.20	853	29	3.79
889	1166	388.88	889	1199	328.17
890	7	3.13	892	4843	1353.13
892	6019	2345.57			

NORTH 1978			NORTH 1979		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	94	76.02	90	272	226.68
102	2	39.95	187	5879	210.51
438	3701	6232.51	316	49	4.01
439	24	20.95	438	2020	3950.89
451	223	6.50	451	2576	25.27
474	131	104.66	474	100	106.44
699	174	1183.57	699	164	1346.32
700	412	286.94	700	204	205.05
701	62	247.54	701	70	345.57
729	409	239.37	726	200	137.12
730	340	76.24	730	159	34.48
793	28	24.24	793	4	6.35
794	7698	2526.67	794	803	302.54
813	10	0.79	810	18	0.58
819	11	10.36	813	21	0.57
829	19	3.11	819	8	11.10
836	48	2.40	836	49	1.92
844	12	1.12	849	51	168.07
849	35	89.98	889	3764	1696.31
889	5272	2462.03	890	35	35.39
890	25	18.13	892	5373	3241.69
892	2426	1855.92	893	2	6.35

NORTH 1980

Spc.	Numb.	Kg.
90	493	353.95
102	4	34.50
187	441	13.23
316	25	0.91
438	4041	8427.50
451	259	4.32
474	346	301.00
478	11	1.80
699	227	1713.50
700	239	213.70
701	91	492.53
726	277	197.90
730	172	53.07
793	60	76.75
794	3924	1334.15
827	12	1.92
836	20	1.86
849	18	50.00
889	7750	4151.10
890	108	101.40
892	3403	3067.00
893	8	19.30

NORTH 1981

Spc.	Numb.	Kg.
90	82	80.65
102	1	14.00
187	12907	370.51
318	30	0.75
324	36	1.95
438	2646	6022.50
439	14	14.90
451	3138	53.25
474	71	74.60
699	206	1605.30
700	150	155.95
701	49	307.50
729	62	53.00
730	20	4.20
793	7	8.80
794	1576	707.45
889	6459	3402.25
890	34	35.50
892	3933	2834.40
893	9	69.50

NORTH 1982

Spc.	Numb.	Kg.
90	157	135.10
187	178	27.93
438	7437	14359.40
439	32	27.50
451	2252	39.85
474	170	162.60
699	314	2487.50
700	228	223.18
701	157	725.90
729	211	178.30
730	65	15.01
793	14	17.90
794	40	13.71
813	31	0.42
836	15	0.72
843	13	0.62
849	17	51.80

NORTH 1983

Spc.	Numb.	Kg.
90	198	168.95
187	75	2.03
438	9495	14244.50
439	17	17.30
451	1726	58.84
474	251	212.90
699	296	2201.80
700	340	324.90
701	108	518.30
711	2	0.20
726	2	0.20
729	132	94.77
730	111	26.60
793	92	112.60
794	4341	1374.44
813	27	0.30
836	16	0.26

889	13326	6167.50
890	17	15.90
892	3977	3590.00
893	6	18.10

849	16	39.90
889	10539	5649.43
890	47	41.20
892	4574	3904.20
893	2	20.50

Spc.	NORTH 1984 Numb.	Kg.
90	150	143.85
102	3	12.00
187	165	5.02
320	9	0.30
438	5373	8043.00
451	1107	28.99
474	150	144.60
699	159	1358.10
700	120	136.75
701	43	169.30
729	80	54.45
730	46	11.65
794	212	67.90
849	11	42.50
889	4855	2673.70
890	22	22.10
892	5371	4572.00

Spc.	NORTH 1985 Numb.	Kg.
90	248	145.90
102	1	9.00
187	896	22.65
272	30	1.10
386	1	0.40
438	5544	7038.90
451	6145	169.66
474	97	85.05
609	26	222.00
699	151	1205.70
700	301	235.72
701	45	177.46
729	100	64.85
730	44	5.35
793	19	13.45
794	1631	455.27
810	45	0.52
813	14	0.23
836	57	1.56
838	42	0.81
843	12	0.49
849	7	22.80
866	13	0.85
889	5352	2653.95
890	86	70.00
892	4482	3606.45
893	9	21.50

NORTH 1986			NORTH 1987		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	102	91.07	90	247	153.18
187	291	6.67	102	2	18.00
438	14452	19046.15	187	7179	251.16
451	696	18.29	438	5723	8829.90
474	27	24.30	474	77	61.10
699	98	966.00	699	58	546.00
700	105	89.00	700	130	96.10
701	37	173.10	701	34	143.60
729	75	50.40	729	61	35.90
730	25	5.80	730	94	12.27
794	103	30.95	793	98	111.10
829	12	2.30	794	1086	405.17
836	43	2.23	810	30	0.48
843	13	0.80	813	12	0.14
849	30	86.90	829	12	1.56
889	3453	1914.90	836	29	1.12
890	11	12.20	849	16	51.70
892	2210	1514.95	863	11	0.73
893	4	11.10	889	2840	1567.40
			890	94	73.70
			892	3047	1832.89

NORTH 1988			NORTH 1989		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	330	265.10	90	243	115.79
91	14	7.27	102	3	29.75
187	1755	52.39	187	257	6.85
316	15	0.64	272	55	0.96
438	7878	13943.81	438	5885	6056.86
451	1149	25.84	439	8	6.01
474	46	25.45	451	2068	76.20
699	59	674.20	474	94	49.40
700	135	121.30	699	41	511.01
701	37	135.60	700	66	58.74
729	89	56.20	701	35	161.98
730	179	23.87	727	11	1.34
794	323	103.76	729	248	117.80
813	11	0.26	730	117	19.19
827	34	5.13	793	9	7.76
836	29	114.00	794	229	78.69
838	12	0.51	810	20	0.24
849	33	102.60	813	45	0.66
889	3722	2116.48	819	13	7.73

890	72	2392.00
892	7274	3215.57

827	12	1.96
829	14	1.55
836	67	2.02
838	9	0.12
843	24	1.45
844	43	1.99
849	24	50.49
853	21	1.33
889	3636	1731.95
890	34	22.64
892	3303	1844.80

NORTH 1990		
Spc.	Numb.	Kg.
90	166	61.91
187	14	0.39
316	7	0.15
438	1197	955.80
451	66	1.43
474	15	5.77
478	2	0.26
699	14	164.95
700	60	48.33
701	14	59.85
729	54	25.87
730	17	1.78
793	4	4.30
794	35	7.43
810	12	0.14
819	3	1.48
829	14	1.35
836	8	0.15
843	8	0.59
853	2	0.24
861	2	0.75
889	1127	489.81
892	553	200.03

NORTH 1991		
Spc.	Numb.	Kg.
90	133	40.88
91	6	2.21
187	38	0.87
227	2	0.12
272	7	0.12
320	2	0.06
373	2	0.24
432	3	0.25
438	423	268.54
451	1299	22.01
474	59	26.45
478	10	1.21
481	127	37.34
699	6	42.55
700	66	59.52
701	15	35.23
729	40	18.43
730	29	4.13
793	5	5.14
794	129	29.39
810	18	0.24
819	6	6.43
820	1	0.46
829	29	4.29
836	15	0.46
838	6	0.11
843	3	0.46
849	9	24.11
853	12	0.51
889	389	136.10
890	1	0.50
892	486	159.68

MAIN 1978			MAIN 1979		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	538	421.82	90	858	704.61
91	365	147.43	91	332	225.04
102	18	141.67	102	41	392.30
150	1	0.34	187	110	3.27
187	2	0.06	272	52	1.57
272	4	0.35	316	54	3.90
316	10	1.28	386	1	1.81
438	3670	6501.43	438	7185	13980.46
451	1	0.03	444	1	0.05
454	3	0.56	451	172	2.61
461	19	1.51	453	8	1.02
474	271	215.69	461	5	0.96
478	16	2.66	474	636	588.96
699	130	914.12	478	72	11.31
700	676	610.77	699	251	1876.87
701	85	272.28	700	687	744.80
711	1	0.14	701	90	306.21
721	1	0.45	716	1	0.05
727	7	3.23	721	3	1.58
729	224	116.07	726	125	81.94
730	1885	297.62	727	15	15.56
793	179	217.53	729	1	0.45
794	14204	5408.93	730	1188	266.16
812	123	3.59	747	1	0.05
813	6	0.36	793	531	813.96
819	2	0.90	794	19482	7945.50
820	3	1.14	810	91	2.33
823	1	0.05	811	1	0.05
829	39	4.29	813	8	0.39
836	30	1.87	820	2	1.59
838	9	0.60	827	18	3.78
849	2	3.18	829	39	4.74
859	1	0.10	836	8	0.38
889	3780	1391.25	838	10	0.49
890	1404	1112.38	849	39	116.36
892	1955	1224.29	853	1	0.05
			889	3445	1261.38
			890	2294	1792.72
			892	4396	3440.84
			893	4	30.40

MAIN 1980			MAIN 1981		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	1	2.00	90	444	518.90
90	432	444.13	91	162	102.20
91	262	160.35	102	29	211.50
102	37	294.70	187	78	2.98
187	266	9.33	230	1	0.01
227	2	0.04	272	51	2.98
272	68	1.73	318	3	0.30
316	59	4.19	324	66	3.86
432	4	1.00	387	1	4.00
438	3742	7864.71	438	4637	10473.50
444	2	0.15	444	1	0.01
451	532	5.45	451	27	1.17
453	4	0.65	454	3	0.60
458	1	0.50	474	430	409.30
461	2	0.30	478	12	2.70
474	562	511.15	699	113	911.00
478	47	9.15	700	287	273.25
481	2	2.00	701	57	240.80
699	209	150.50	727	6	4.90
700	630	570.93	729	40	21.36
701	71	229.15	730	319	73.95
721	1	0.10	793	209	394.85
726	85	37.40	794	23844	10643.35
727	10	9.30	809	1	0.20
730	1136	237.04	810	5	0.23
793	5476	6360.93	822	15	2.60
794	17233	9163.98	827	5	1.00
810	21	0.64	836	1	0.10
813	2	0.02	849	10	34.00
814	0	0.10	889	2785	1231.90
827	46	6.28	890	2342	1894.80
836	1	0.01	892	4592	3617.50
838	2	0.02	893	2	41.50
849	6	17.00			
853	0	0.02			
859	1	0.10			
889	3413	1192.43			
890	2422	1875.26			
892	3698	3076.70			
893	13	143.50			

MAIN 1982			MAIN 1983		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	511	500.70	90	682	654.45
91	258	169.05	91	242	157.30
102	40	322.50	102	39	256.45
187	750	25.84	187	1461	40.11
316	21	2.10	438	5246	9782.70
438	5181	10949.40	451	114	4.36
451	562	8.38	699	145	1017.60
474	840	747.20	700	386	364.05
478	23	3.15	701	73	276.10
699	223	1445.50	730	434	123.07
700	539	474.40	793	3726	3382.30
709	76	273.10	889	2884	1189.15
729	94	52.80	890	2761	23344.65
730	489	115.80	892	7451	6283.00
793	435	557.90	893	15	119.50
794	18860	6766.54			
829	30	5.80			
849	21	54.00			
889	2734	1048.70			
890	2229	1790.60			
892	7039	5797.00			
893	9	73.50			

MAIN 1984			MAIN 1985		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	1026	980.15	90	574	551.74
91	206	136.90	91	202	120.20
102	37	33.60	102	27	268.95
187	585	15.19	187	1162	34.33
272	63	1.62	316	64	3.41
316	27	2.22	438	3868	6238.35
320	66	2.22	451	970	11.26
438	3909	7479.45	474	446	332.80
451	281	4.47	478	56	7.70
474	627	533.05	699	125	1016.80
478	52	8.80	700	299	250.50
481	253	55.80	709	44	187.40
699	196	1631.85	730	196	41.14
700	352	317.95	793	639	665.35
701	81	292.85	794	22272	8387.28
729	83	49.95	810	38	0.98
730	389	98.07	829	23	281.00
793	464	560.30	849	12	29.70

794	15685	6368.10	889	21.43	963.70
810	23	0.40	890	2403	1745.35
829	21	370.00	892	7268	4615.85
849	13	32.55	893	8	61.50
889	4086	1810.50			
890	3274	2817.45			
892	9589	7227.52			
893	7	42.55			

Spc.	MAIN 1986 Numb.	Kg.	Spc.	MAIN 1987 Numb.	Kg.
27	18	28.50	90	379	360.88
90	407	449.20	91	101	62.50
91	105	75.15	102	22	149.60
102	13	97.20	187	1311	46.46
187	1139	34.79	272	104	2.64
272	33	0.54	316	24	1.32
438	9216	14597.60	386	9	11.50
451	52	1.75	432	12	2.10
474	260	182.07	438	5207	8914.25
478	69	7.55	451	19	0.53
481	136	44.98	474	339	271.22
699	56	477.50	478	120	14.60
700	159	123.60	481	35	12.70
701	27	78.90	699	94	876.50
729	28	19.15	700	147	111.21
730	229	47.05	701	34	192.70
793	339	304.60	729	56	27.00
794	12106	6373.49	730	233	34.51
810	70	0.75	793	74	117.60
849	17	36.70	794	4981	2316.86
889	3034	1499.45	810	37	0.51
890	899	679.10	829	35	2.67
892	9874	6884.61	849	19	51.25
893	2	22.10	889	2016	872.45
			890	1302	1024.75
			892	8283	5088.45
			893	4	17.00

MAIN 1988			MAIN 1989		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	3	11.00	27	4	5.91
90	328	295.00	90	776	533.35
91	74	49.35	91	102	52.76
102	7	56.10	102	15	139.76
187	185	4.05	187	510	14.48
272	30	0.56	316	21	0.53
316	23	0.66	438	13281	20300.68
438	2733	4244.40	451	457	18.31
451	291	3.21	474	251	143.02
474	222	167.05	478	54	5.67
478	63	7.45	699	35	374.95
699	63	616.10	700	141	120.93
700	135	111.23	701	39	156.25
701	40	170.40	729	95	58.60
729	30	19.22	730	445	67.38
730	110	14.22	793	633	864.63
793	152	156.70	794	7578	2998.02
794	14696	7697.86	810	35	0.51
810	31	0.36	827	44	6.30
827	53	5.78	829	46	5.35
849	14	39.40	836	32	0.95
889	1509	714.15	849	36	111.82
890	880	703.50	889	3039	1209.15
892	3699	1930.00	890	729	515.23
893	5	16.70	892	119.71	506.86
			893	15	172.33

MAIN 1990			MAIN 1991		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	436	342.38	90	355	246.63
91	45	23.29	91	55	22.44
102	10	64.79	102	10	36.86
187	66	17.93	187	2853	52.44
272	35	0.83	272	336	3.21
316	34	0.77	316	243	4.71
384	10	12.96	320	31	0.72
432	41	10.75	385	13	11.55
438	104.24	12217.41	438	18121	17009.73
451	34	0.77	451	257	4.00
474	379	257.46	474	224	93.60
478	153	18.92	478	141	13.50
481	206	33.03	481	87	19.27

699	41	434.86	699	17	211.30
700	60	46.44	700	169	133.50
701	23	103.60	701	38	149.57
729	45	16.73	729	49	16.76
730	233	32.54	738	133	17.28
793	245	258.00	793	213	201.15
794	115.37	5708.67	794	4331	1567.62
829	34	6.12	810	44	0.57
849	7	20.85	829	121	15.09
889	1481	598.35	849	17	40.60
890	962	660.44	889	1630	578.78
892	4885	2426.09	890	134	78.11
			892	3314	1512.09
			893	5	63.30

DEEP 1978			DEEP 1979		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
90	5	2.75	27	53	88.01
438	330	606.26	90	25	20.75
474	102	103.97	91	1	2.27
478	12	0.76	102	5	64.89
699	45	246.98	373	42	7.14
700	18	17.84	386	14	24.52
701	5	24.06	432	145	70.80
727	8	6.65	438	1548	2633.32
729	4	0.65	474	309	240.29
730	67	12.20	478	81	16.48
793	47	61.25	481	5386	2439.01
794	7141	2881.99	483	1	0.54
829	5	0.55	699	128	672.75
836	1	0.10	700	200	116.64
889	119	18.85	701	15	45.54
890	57	40.87	727	7	8.17
892	148	246.57	728	1	0.45
893	1	3.80	793	42	68.77
			794	12514	5337.19
			829	3	0.14
			849	8	23.82
			889	153	67.70
			890	5	4.54
			892	592	1793.24
			893	3	18.61

DEEP 1980			DEEP 1981		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	229	417.50	27	171	271.75
90	36	44.30	90	42	54.10
102	14	175.00	102	10	113.00
167	2	9.00	167	44	161.25
316	24	1.58	272	136	2.21
373	58	12.25	387	18	31.20
386	55	74.95	432	174	54.35
432	284	101.20	438	1539	4131.25
438	662	1606.45	474	394	345.15
458	2	13.50	478	108	23.95
474	516	374.30	481	1691	656.35
478	220	43.87	699	140	836.75
481	4624	2424.00	700	46	29.45
699	272	1540.00	701	8	26.00
700	131	89.20	793	1651	1230.17
701	24	78.00	794	45223	18043.83
730	102	25.00	889	31	8.40
793	31	75.25	890	37	33.00
794	22277	9503.45	892	785	2359.10
827	25	3.50	893	5	27.80
889	141	41.30			
890	58	51.50			
892	1335	3221.50			

DEEP 1982			DEEP 1983		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	140	226.30	27	217	351.50
90	41	49.00	90	14	23.20
91	21	14.20	94	8	3.80
96	8	13.60	102	7	87.80
102	11	144.00	202	9	0.20
272	61	2.17	272	114	2.68
373	98	16.27	318	8	1.35
386	53	70.30	369	37	7.20
432	315	110.60	373	9	1.10
438	485	1072.00	386	20	31.60
474	600	410.20	432	217	69.20
478	210	37.10	438	15	33.00
481	2396	521.10	478	59	10.80
699	113	729.00	481	4013	796.40
700	66	35.60	483	15	2.50
701	9	29.90	699	90	584.10

730	24	5.45	727	10	11.00
793	72	94.80	793	17	60.20
794	24394	9761.83	794	10408	4883.77
849	15	45.30	890	91	89.80
889	53	18.20	892	722	2127.50
890	185	176.70	893	1	14.00
892	1344	3355.60	980	1	0.20
893	6	213.50			

DEEP 1984			DEEP 1985		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	143	236.95	27	226	381.05
90	38	44.91	90	37	42.30
91	34	18.50	102	8	122.50
102	11	150.50	202	23	0.95
202	45	1.60	272	113	4.10
227	3	0.20	373	78	11.37
230	2	0.15	386	44	58.45
358	13	2.40	432	142	49.55
368	21	3.95	438	41	80.00
373	68	10.04	474	262	203.50
386	35	45.85	478	179	25.35
432	282	96.40	481	4913	1490.83
438	256	451.50	699	155	1228.70
453	7	3.20	700	9	4.60
458	3	10.50	701	8	30.55
474	337	281.40	793	24	63.50
478	87	14.90	794	10705	4898.05
481	4007	1122.00	849	8	24.55
699	99	621.00	889	15	5.30
700	50	34.45	890	369	305.50
701	7	11.30	892	1572	3033.75
727	6	5.30	893	6	55.25
730	20	6.05			
793	96	100.65			
794	8851	4119.65			
889	19	8.30			
890	38	34.05			
892	1090	2358.50			
893	3	22.50			

DEEP 1986			DEEP 1987		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	192	287.70	27	81	127.70
90	6	10.30	90	6	12.40
102	5	53.00	102	8	88.50
167	306	1194.27	167	2	2.43
272	66	1.54	200	7	0.24
300	8	1.40	202	10	0.83
316	12	1.73	227	8	0.44
373	20	3.83	272	59	1.09
384	17	26.10	316	4	0.27
432	74	24.90	369	4	0.32
474	297	259.10	373	33	4.85
478	99	10.95	385	2	5.10
481	1129	304.10	386	17	36.90
483	5	1.60	432	105	23.90
699	48	424.20	474	201	135.15
700	3	1.70	478	88	13.18
701	19	104.70	481	236	83.15
730	5	1.10	482	3	0.70
793	14	27.75	699	47	252.50
794	6881	3664.70	701	2	6.30
829	17	2.60	793	6	18.10
889	17	8.80	794	3034	1875.20
890	290	229.90	829	6	1.81
892	964	2125.50	889	6	2.80
893	1	12.50	890	298	224.40
			892	598	1180.50
			893	2	18.20

DEEP 1988			DEEP 1989		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	47	73.90	27	44	75.41
90	3	2.20	90	5	4.10
102	11	171.00	91	3	0.47
167	95	279.50	102	1	12.00
202	7	0.52	272	26	0.51
227	4	0.20	316	2	0.06
272	22	0.66	372	11	1.66
367	6	0.80	373	12	1.85
373	6	0.90	385	5	5.26
384	1	3.00	432	20	2.68
386	2	5.00	438	398	425.42
432	25	13.10	458	1	1.96

438	27	33.80	474	104	62.82
474	196	187.00	478	32	3.35
478	37	5.10	481	403	122.32
481	379	181.90	699	12	126.75
483	7	2.20	700	20	13.81
699	32	245.50	701	5	12.67
700	5	4.00	729	4	0.82
701	1	2.60	730	11	4.40
730	5	1.40	793	9	9.59
793	6	18.20	794	628	318.44
794	5051	2860.37	810	3	0.08
827	4	2.05	828	1	0.99
849	1	2.60	829	4	0.46
889	20	12.85	849	1	4.85
890	87	63.90	889	102	51.41
892	580	995.40	890	24	16.78
			892	218	235.03

DEEP 1990			DEEP 1991		
Spc.	Numb.	Kg.	Spc.	Numb.	Kg.
27	94	166.20	27	62	81.08
90	8	12.60	90	21	23.89
94	1	0.25	94	4	1.82
102	9	125.10	102	8	110.05
227	3	0.26	202	8	0.21
272	10	0.28	227	9	0.46
316	3	0.09	272	67	1.01
318	1	0.05	316	85	1.96
373	28	6.23	320	10	0.40
384	1	1.70	368	5	0.48
385	2	4.45	373	13	1.88
386	2	4.85	384	2	5.20
432	70	14.41	385	22	36.10
438	11	5.95	432	76	16.03
453	2	1.05	438	13	11.23
474	222	186.74	453	5	1.53
478	54	8.94	474	472	327.83
481	929	299.81	478	121	15.56
483	8	1.75	481	1174	392.84
699	26	225.65	483	6	1.76
701	1	3.30	699	26	303.50
727	4	1.70	727	5	1.71
730	4	0.66	730	4	0.45
793	2	5.30	793	3	2.97
794	672	237.29	794	852	257.56
827	7	2.18	829	22	3.56

829	9	1.46	849	1	3.85
849	2	2.35	889	149	66.54
889	44	18.17	890	493	273.21
890	104	64.20	892	897	662.00
892	1107	1136.50			

APPENDIX 2

This appendix contains maps showing the spatial assemblage distribution and bottom temperatures recorded in the different sampling stations surveyed over the fourteen years (1978-1991) of the study; each dot represents the exact geographical position of the sampled station.

For each year, 2 maps are shown on the same page; on the left, the different colours indicate sampling stations identified as being similar in faunal composition. They cluster in contiguous areas that define the boundaries of the four assemblages ; i.e orange = Coastal, black = North, red = Main and yellow = Deep. In the same map, the background bathymetry depths (in shades of blue) are: white (100m), pale blue (200m), dark turquoise (300m), navy (400m) and dark blue (800m and deeper).

The map on the right shows the bottom temperature measured at that station when the fish trawl was towed. The scale used for the colour dots in this map is (in °C, BT = Bottom Temperature):

BT < -1 = light blue	-1 < BT <= 0 = purple
0 < BT <= 1 = dark blue	1 < BT <= 2 = green,
2 < BT <= 3 = yellow	3 < BT <= 4 = orange,
BT > 4 = red.	

Note the grouping of the Main Assemblage by the shelf-break and the colder bottom temperatures in the last years of the study.

